Physical and Biological Factors Affecting Pacific Herring Egg Loss in Prince William Sound, Alaska

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by

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PHYSICAL AND BIOLOGICAL FACTORS AFFECTING PACIFIC HERRING EGG LOSS IN PRINCE WILLIAM SOUND, ALASKA

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Abstract

The biomass of Prince William Sound herring (*Clupea pallasi*) is estimated from egg deposition surveys. Because surveys occur after spawning, a correction for egg loss is required. I constructed ANOVA models based on environmental factors to estimate the egg loss correction in 1990-1991 and 1994-1995. The models explained 52% to 85% of the data variation. Depth of spawn was the primary factor determining egg loss, and air exposure could be substituted for depth. The correction factor was estimated at 33%. The total loss of eggs from spawning to hatching ranged from 67.40% to 100% averaging 76.06%. Two processes affecting egg loss, wave action and fish predation, were also examined. Typical wave energies were not found to contribute significantly to egg loss, but a threshold wave energy may exist beyond which egg loss is high. Consumption of eggs by greenling (*Hexagrammidae*) was estimated at 2.2% to 8.5% of the total spawn.

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Introduction

The reasons for the failure of the Prince William Sound herring (*Clupea pallasi*) fishery in 1993-1996 are not well understood at the present time; however, a combination of physical and biological processes may be involved. Physical processes (Royer 1986) may be important for fish stocks, through effects on growth and mortality at all stages of life. Herring recruitment in particular show strong relationships with the environment (e.g. Zebdi 1991, Wespestad 1991).

Physical variables related to habitat type (e.g. exposure to waves, exposure to air, depth, substrate type) may induce inter-annual variability in egg loss and survival. Biological interactions may also be involved, in that bird species (glaucous-winged gulls, surfbirds), invertebrates (crabs, seastars), marine mammals, and fishes (sculpins, salmonids, greenling) are found in the nearshore zone and known to be predators of herring eggs and juveniles. Finally, the *Exxon Valdez* oil spill of 1989 may have affected adult and juvenile health, egg viability, and genetic composition of Prince William Sound herring.

The Alaska Department of Fish and Game (ADF&G) has been analyzing factors affecting the survival of Pacific herring eggs in Prince William Sound since the occurrence of the *Exxon Valdez* oil spill. Mapping and enumeration of spawn deposition using aerial and dive surveys dates back to 1972 (Funk 1993). Estimates of the amount of spawn deposited are used to calculate the total spawning biomass of Pacific herring.

Because the spawn deposition surveys typically occur some days after spawning, some loss of eggs occurs, requiring a correction factor. In the past a correction factor of 10% has been used; however, recent research on herring in Prince William Sound and British Columbia (Biggs-Brown and Baker 1993, Schweigert, pers. comm.) suggests that egg loss is variable across years and across sites and higher than previously thought (Wilcock and Brown 1994). Biggs-Brown and Baker (1993) determined a range of correction factors from 10 to 15% for 1990-91 Prince William Sound data.

Biometrics and modeling assistance for the egg loss study was contracted to the School of Fisheries and Ocean Sciences (SFOS), University of Alaska Fairbanks (UAF) in late 1994, under the Herring Natal Habitats project #95166 from *Exxon Valdez* oil spill restoration funds. The goal of this project is to build a sound-wide embryo survival model including factors such as habitat type, egg density, predation, and meteorological conditions.

This document summarizes the findings of the Pacific herring egg loss modeling study. In Chapter 1 of this report, I develop a model of herring egg loss based on physical and biological variables. In Chapter 2, I apply the egg loss model to predict the initial number of eggs at selected spawn deposition transects in 1995. In Chapter 3, I measure the effects of wave energy on egg loss in 1995. Finally, in Chapter 4, I estimate consumption of herring eggs by fish predators in 1995.

Chapter 1. Factors affecting Pacific herring egg loss in Prince William Sound.

1.1. Introduction

Previous studies have found that many factors can contribute to Pacific herring egg loss. Large proportions of egg loss in the intertidal zone have been attributed to bird predation (Cleaver and Franett 1946; Outram 1958; Steinfeld 1971; Haegele and Schweigert 1989; Haegele and Schweigert 1991). Subtidally, marine mammal (Haegele and Schweigert 1989) and invertebrate predation (Haegele and Schweigert 1989; Haegele 1993) have been implicated as sources of herring egg loss. Wave action is also considered a major cause of egg loss (Hart and Tester 1934; Hay and Miller 1982). Both physical (wave action) and biological (predation) processes were included in Prince William Sound egg loss modeling.

Prior analysis

Studies of egg loss for herring in Prince William Sound were conducted in 1990, 1991, 1994 and 1995. The focus of the 1990 and 1991 studies was to examine the effects of oil on egg loss, and did not include collection of data relating egg loss to habitat, environmental conditions, or predation. In 1990 and 1991, the major auxiliary variable used in analyses was depth, although vegetation type was used to estimate calibration

factors for different divers. The 1994 study collected some information regarding habitat factors, but the primary research effort occurred in 1995.

Methods and results from the 1990 and 1991 studies are found in Biggs-Brown and Baker (1993). Analyses of covariance were conducted with egg abundance as the dependent variable, transect and depth as factors, and days as the covariate, along with several interaction terms; all main effects and interactions were statistically significant. The egg loss model explained about 70% of the variability in the data, with most of the variability explained by transect-related parameters. The authors speculated that oil itself was probably not involved in the differences in egg loss, because very little was present at that time. Because transects in previously-oiled areas were in more exposed locations, the authors suggested that the significant effect of oil actually indicated that wave or tidal action was the most important factor determining egg loss in Prince William Sound.

Current analysis

In our study, we revisit the analyses of Biggs-Brown and Baker (1993) and attempt to explain the variability among transects by habitat differences. Because transects represent specific locations, the use of transects as a factor does not provide understanding of the possible mechanisms which affect egg loss rates. In this study, I analyzed both physical and biological components to determine their individual contribution to egg loss. The physical variables included depth, time of air exposure over

incubation, spawning substrate, and egg loss due to wave action. Biological variables included: predation by fish, predation by birds, and the effect of vegetation type upon which eggs are deposited. The objective of this report is to use the egg loss data to determine which habitat variables (both physical and biological) affect Pacific herring egg loss in Prince William Sound, and to develop a model for predicting egg loss based on those variables.

1.2. Materials and Methods.

Habitat variables

Data sets (1990, 1991, 1994 and 1995) were acquired from Alaska Department of Fish and Game, in Cordova Alaska. Habitat variables of interest were evaluated as to importance in affecting egg loss; consequently, transects from all years were classified by wave exposure, oiled or unoiled condition, substrate type, vegetation type, depth, and time of air exposure over incubation. Additional variables in 1994 were average bird abundance, average abundance of glaucous winged gulls and cumulative loose eggs observed at each transect. In 1995 average bird abundance, average glaucous winged gull abundance, and an index of fish predation were additional variables used.

Wave exposure

Since no data were collected in 1990-91 or 1994-95 that directly measured the force of wave action at each transect, a dichotomous categorical classification was developed (wave-exposed/protected). This variable was used to classify transects as exposed to waves or protected from waves based on the observations of biologists in the field. In most cases the difference between the two categories was whether the transect was within an embayment or on a headland.

Oiled/Unoiled

This variable was based on the trajectory of oil released from the *Exxon Valdez* spill in 1989: oiled transects were in the path of spilled oil, while unoiled transects were not. Since all unoiled transects occurred in the north sound and all oiled transects occurred in the south sound, the presence of oil is confounded with a north/south location factor. In 1994 and 1995, low abundance of spawning herring in Prince William Sound resulted in the majority of spawning occurring in the southern half of the sound on Montague Island. Since egg loss transects were only installed on Montague Island, oiled/unoiled variable was eliminated as a factor in both 1994 and 1995.

Substrate type

The substrates observed at egg loss transects during the study were classified as rocky, boulder, gravel, sand and mud. In 1991 and 1995 all transects were on rocky substrates, and in other years most transects were located on rocky substrates.

Kelp type

This variable had two categories based on the dominant vegetation in each of the sampling quadrats: 1) any type of large brown kelp was dominant in the quadrat, or 2) some other type of vegetation was dominant. This variable was developed to account for differences in egg adherence due to the slick surface of large brown kelp fronds observed by divers.

Depth

Since quadrats for sampling egg loss were at fixed depths each year, depth was used as a habitat variable. However, the depths used in 1994 and 1995 were different than those used in 1990 and 1991, so this variable was not directly comparable among all years.

Air exposure

A computer tide program was used to calculate the cumulative time of air exposure in hours over the entire incubation period for each depth. This variable was calculated because air exposure may be a principal factor relative to egg loss mechanisms such as desiccation or bird predation.

Bird abundance

The abundance of birds in 1994 and 1995 was measured by US Forest Service, Copper River Delta Institute personnel as a part of the Avian Predation on Spawn project (EVOS #96320-Q), which estimated the total number of herring eggs consumed by birds

over the incubation period. The methods for collecting this information were not the same both years, so the results may not be comparable.

Loose eggs

The cumulative number of loose eggs was an additional set of information collected at each transect. Divers counted and recorded the number of unattached and floating eggs they observed at each quadrat. However, this information was collected only in 1994.

Fish Predation

An index of fish predation was developed for 1995 transects using catch per unit effort of fish species weighted by egg consumption. Gillnet sampling for fish predators was carried out at all transects in 1995, and captured fish were later analyzed for stomach contents in the laboratory.

Since the original egg loss study had not been designed to examine these habitat variables, an unbalanced design resulted. This imbalance predetermines the analyses that were performed, as not all factors can be compared with all others. For example, in 1994 all transects that were wave-exposed occurred on rocky and boulder substrates, therefore the effect of exposure could not be compared for all substrates. In 1995 an attempt was made to define habitat variables of interest prior to the sampling season and then balance the sampling design around those variables. A summary of the habitat variables available for each year can be found in Table 1, and the locations and habitat classifications for

Table 1. Summary of habitat variables available for each year of the egg loss study. + indicates these variables are confounded in 1994.

Habitat Variable \ Year	1990	1991	1994	1995
Depths (ft)	-30, -15, -5, 0, 1, 5	-15, -5, 0, 1, 5	-10, -3, -2, 0, 2, 3	-5, -1, 0, 1, 3, 5
Air exposure	X	X	X	X
Wave exposure	X	X	X+	X
Oiled/Unoiled	X	X		
Year	X	X	X	X
Substrate	X		X+	
Kelp Type	X	X	X	X
Average bird abundance			X	X
Average gull abundance			X	X
Cumulative loose eggs			X	
Fish abundance				X

each transect can be found in Figure 1. Egg loss models were developed for each year individually, as well as for combinations of the years. In each case graphical analysis served as a guide for development of egg loss models.

Preliminary Analysis

The first step in analyzing the egg loss data from Prince William Sound was to repeat the analyses performed by Baker and Biggs on the 1990 and 1991 data using analyses of covariance techniques (Baker and Biggs, 1993). This analysis was performed using the SAS statistical package, and assured that analyses are complementary. For the analyses involving the habitat variables and the 1994 and 1995 data, SYSTAT was used. All databases have been transferred from Rbase and maintained in Excel spreadsheets.

Graphical Analysis

Analysis of egg loss was carried out using two dependent variables; log transformed egg abundance data, and the egg loss rates (Z) developed from linear regressions. In graphical analysis of ln(egg abundance) data, transformed egg counts were plotted against days since spawn for each transect, showing the egg loss rate at each depth.

Analyses of egg loss assume that the instantaneous rate of egg loss (Z) is constant over days. Reference day 0 is considered to be the beginning of the spawning period. If $N(t)$ is the number of eggs at reference day t and N_0 is the number of eggs at reference day 0, then

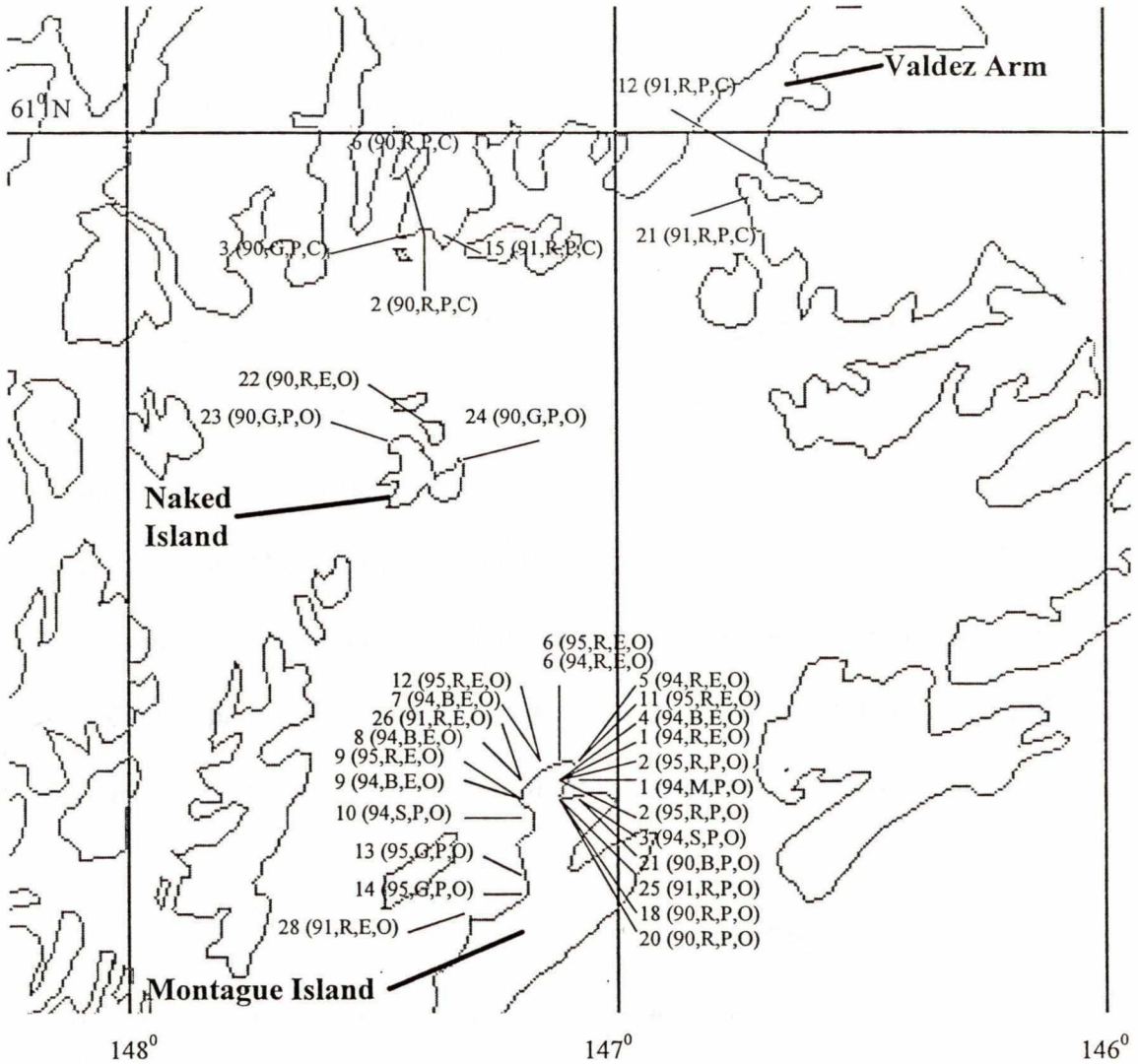


Figure 1. Map of Prince William Sound, Alaska showing egg loss transects. R=rocky, B=boulder, G=gravel, M=mud, S=sand substrates. E=wave exposed, P=wave protected. O=oiled, C=unoiled.

$$N(t) = N_0 e^{-Zt} e^{\varepsilon}$$

where ε is a random error term with mean 0 and constant variance. Taking the logarithm of this equation, one obtains

$$\ln N(t) = \ln N_0 - Zt + \varepsilon$$

showing that a linear regression of ln(egg abundance) versus days can be used to estimate $\ln N_0$ and Z from the y-intercept and slope respectively.

Graphical analyses of the negative of egg loss rates (-Z) was then performed for each of the habitat variables. Each egg loss rate represents the slope of the linear regression at one depth at one transect of ln(egg abundance) against days since spawn. Since a positive egg loss rate (Z) implies negative egg loss, graphical analyses and summaries were conducted using the negative of the instantaneous egg loss rate (-Z). Thus; more negative egg loss rates correspond to higher egg loss, an intuitively satisfying result. Both depth and air exposure were used as independent variables in the graphical analyses to determine which variable is more useful in predicting egg loss rates.

Analyses of Covariance

In these analyses, ln(egg abundance) was used as a dependent variable with days since spawn as the covariate in an analysis of covariance. The other predictors used in the analysis of covariance were the habitat variables, so that

$$\ln N(t) = \ln N_0 - Zt + \alpha_i + \beta_j + ... + \varepsilon.$$

Factorial Analyses

Modeling of habitat variables was carried out using the egg loss rates (Z). Egg loss rates were used as dependent variables in analysis of variance models, where

$$Z=\mu+\alpha_i+\beta_j+\gamma_k+(\alpha\beta)_{ij}+....+\varepsilon.$$

Independent variables included the habitat variables, predation variables and year. Factorial analyses of these variables were performed, sequentially removing insignificant factors. In most cases the resulting models explained a significant portion of the variability in egg loss rates.

Factorial analyses were also performed on egg loss rates, using air exposure as a covariate in the place of depth, and the habitat variables as factors, with the equation

$$Z=\mu+\alpha A_E+\beta_j+\gamma_k+....+\varepsilon.$$

Air exposure was used in the place of depth to determine which term was the most parsimonious in explaining variability in egg loss rates.

Models with air exposure in the place of depth were then compared to models containing only the depth variable using an F-test of the sums of squares to determine if there were significant differences between the two models. Models with air exposure were compared to models with depth across all data sets used in the factorial analyses.

The results of all statistical analyses were then compared to determine the best model for herring egg loss. The R^2 values for each model from factorial analysis were compared to three simple models: a model containing only the depth term, a model

containing only the air exposure term, and a model containing both transect and depth. The R^2 values for these four types of models were compared over all data sets examined, as well as averaged across all data sets. A model was then recommended based on its R^2 value and the consistency of its significance in factorial analyses.

Because of the unbalanced nature of the study design, various subsets of the data were modeled using these analysis of variance techniques. For example, the rocky substrate type, represented by the most transects, was analyzed independently and as part of the entire data set. This eliminated noise associated with the substrate variable, while using the largest available data set.

Data from individual years as well as combinations of years were analyzed to attain the best possible model of egg loss for Prince William Sound. The two years 1990 and 1991 and two years 1994 and 1995 were each combined for analysis. Then data from Montague Island transects (representing previously oiled locations) only were combined over all four years for analysis.

A special analysis to separate the effects of the kelp type variable and the depth variable was performed on egg loss rates from subtidal depths only. Subtidal egg loss rates were compared between the two kelp types using analysis of variance, to determine the significance of the kelp type variable.

1.3. Results

1.3.1. 1990 Analyses.

Egg loss sampling during 1990 took place at nine transects in both previously oiled (southern PWS) and unoiled (northern PWS) areas (Figure 1). Egg loss quadrats were placed at six depths relative to mean low water: -30 ft, -15 ft, -5 ft, 0 ft, 1 ft, and 5 ft, although most transects were not sampled at either of the two deepest depths (Table 2).

Graphical Analysis

Egg loss rates in 1990 ranged from 0.244 to -0.025 with an average of 0.078 and a standard error of 0.011 (Table 2, Figure 2), with about 62.5% of the egg loss regressions significant at the 0.05 level. Egg loss rates at wave-exposed transects appear to increase more sharply with depth than at protected transects in 1990 (Figure 3). This difference is not as distinct when egg loss rates were plotted against air exposure. The wave-exposed category was represented by only one transect in 1990, while the protected category included eight transects.

Egg loss rates in 1990 also differed at oiled and unoiled transects (Figure 4). When plotted against both depth and air exposure, egg loss rates were substantially higher at oiled transects than at unoiled transects.

The most noticeable pattern in data in the substrate categories is the decrease in egg loss rates with increasing depth in the rocky substrate (Figure 5). The rocky substrate

Table 2. Summary of 1990 egg loss regressions from each transect by depth. R=Rocky substrate, G=Gravel substrate, B=Boulder substrate, P=wave-protected, E=wave-exposed, O=oiled area, and C=unoiled area.

Depth	Transect / Habitat classifications	22 O,E,R	2 C,P,R	6 C,P,R	18 O,P,R	20 O,P,R	3 C,P,G	23 O,P,G	24 O,P,G	21 O,P,B
5	slope (-Z)	-0.171					0.003	-0.134	-0.088	
	intercept	6.301					3.115	5.212	4.435	
	R^2	0.408					0.000	0.476	0.328	
	p-value	0.000					0.887	0.000	0.000	
1	slope (-Z)	-0.116	-0.110	-0.035	-0.244		-0.005	-0.010	-0.035	-0.169
	intercept	6.817	4.772	4.869	7.553		4.770	3.112	1.591	7.136
	R^2	0.405	0.136	0.042	0.482		0.001	0.001	0.012	0.515
	p-value	0.000	0.010	0.100	0.000		0.777	0.769	0.434	0.000
0	slope (-Z)	-0.110	-0.020	-0.094	-0.231	-0.103	-0.043	-0.085	-0.121	-0.108
	intercept	6.936	3.176	6.143	7.414	0.733	5.585	2.394	3.895	6.530
	R^2	0.414	0.007	0.353	0.516	0.096	0.112	0.079	0.217	0.386
	p-value	0.000	0.557	0.000	0.000	0.079	0.007	0.031	0.000	0.000
-5	slope (-Z)	-0.020	0.002	0.018	-0.151	-0.129	-0.030	-0.016	-0.088	-0.163
	intercept	5.808	4.938	5.046	3.272	3.457	3.444	0.503	5.053	6.496
	R^2	0.049	0.001	0.056	0.201	0.193	0.025	0.004	0.281	0.281
	p-value	0.090	0.772	0.057	0.005	0.003	0.214	0.645	0.000	0.000
-15	slope (-Z)	-0.040	0.025	0.021		-0.064	-0.035	-0.150	-0.141	-0.129
	intercept	6.337	3.814	4.499		3.889	5.075	3.168	2.930	4.822
	R^2	0.189	0.028	0.069		0.154	0.108	0.262	0.185	0.287
	p-value	0.000	0.174	0.029		0.005	0.008	0.001	0.003	0.000
-30	slope (-Z)		-0.003	0.006						
	intercept		4.042	4.171						
	R^2		0.001	0.007						
	p-value		0.795	0.509						

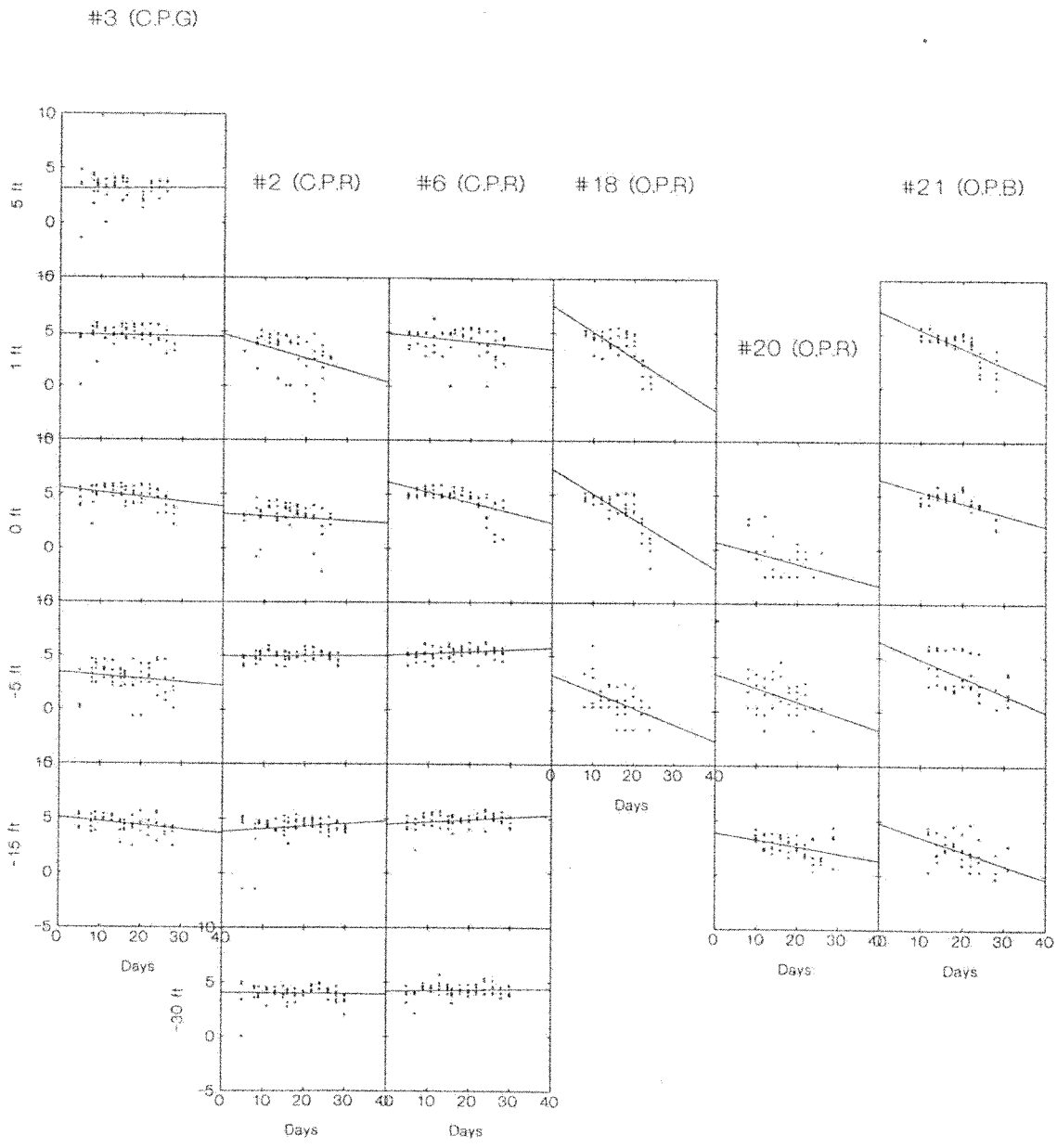


Figure 2. Regressions of ln(egg abundance) against days since spawn for 1990 transects. The estimate of the egg loss rate (Z) for each depth is represented by the line in each graph. C=unoiled, O=oiled, R=rocky substrate, G=gravel substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.

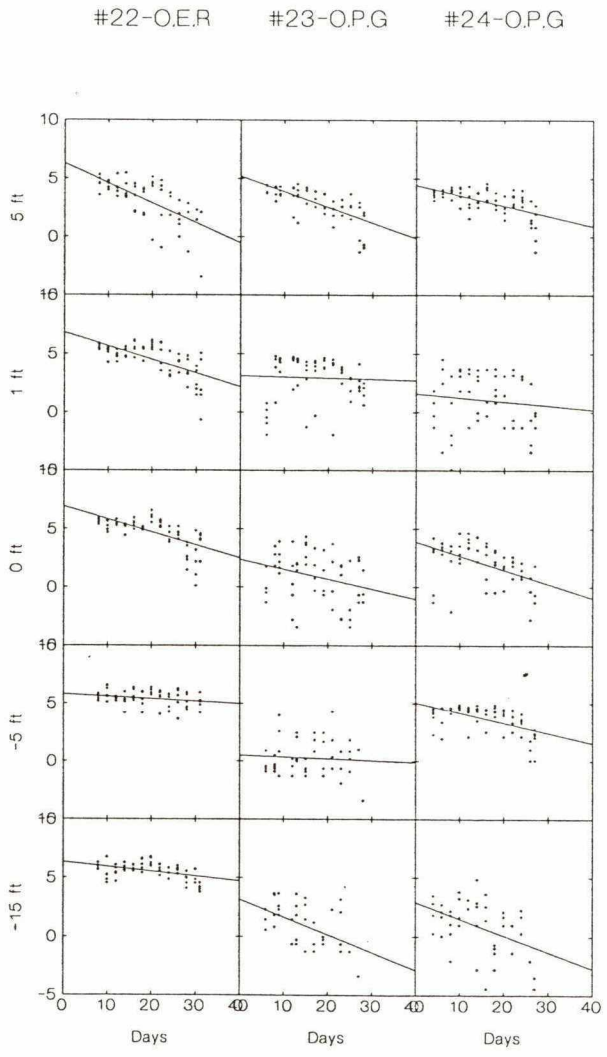


Figure 2 (continued). Regressions of ln(egg abundance) against days since spawn for 1990 transects. The estimate of the egg loss rate (Z) for each depth is represented by the line in each graph. C=unoiled, O=oiled, R=rocky substrate, G=gravel substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.

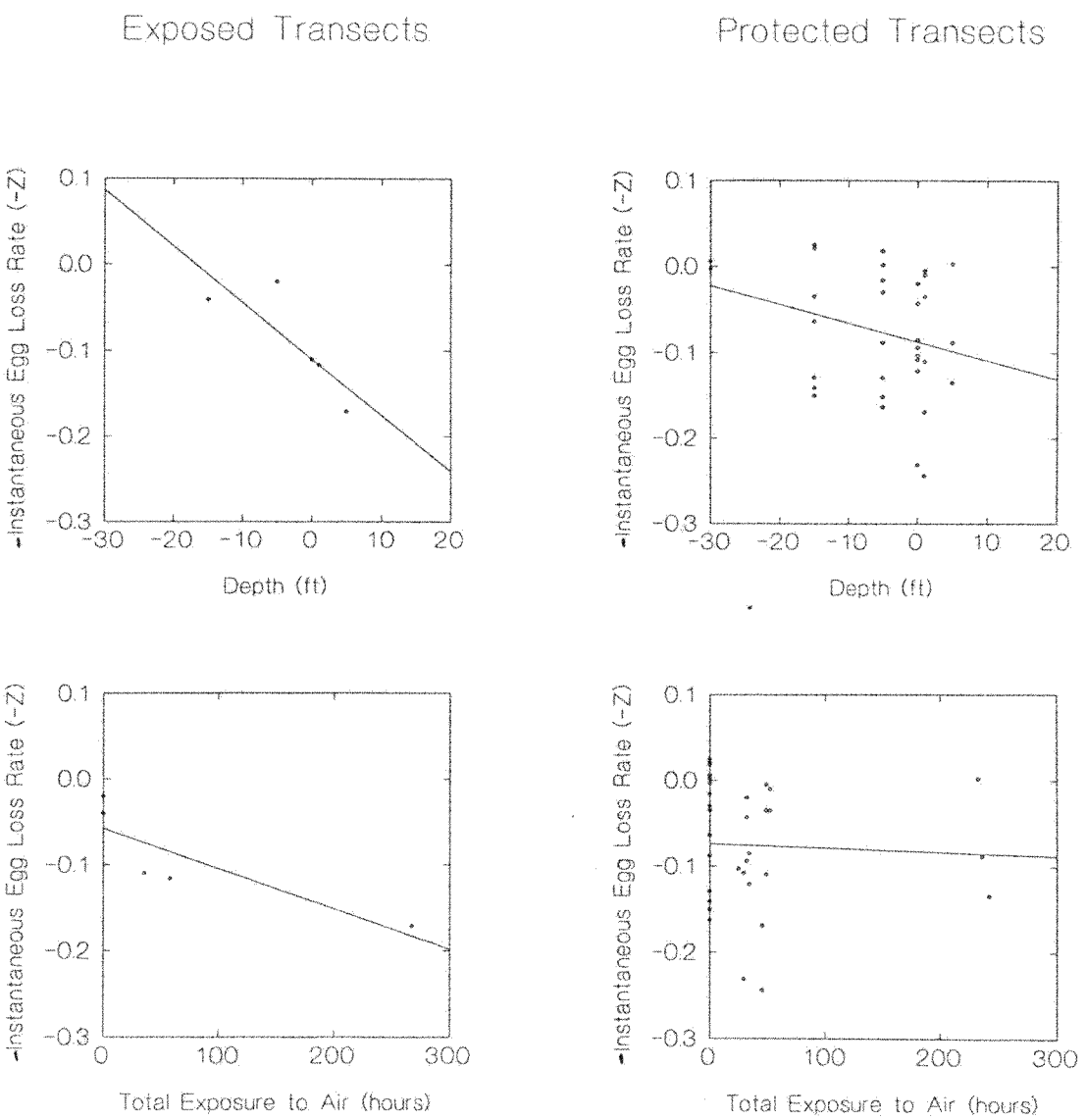


Figure 3. Egg loss rates for wave-exposed and wave-protected transects in 1990. Egg loss rates are plotted against both depth and air exposure.

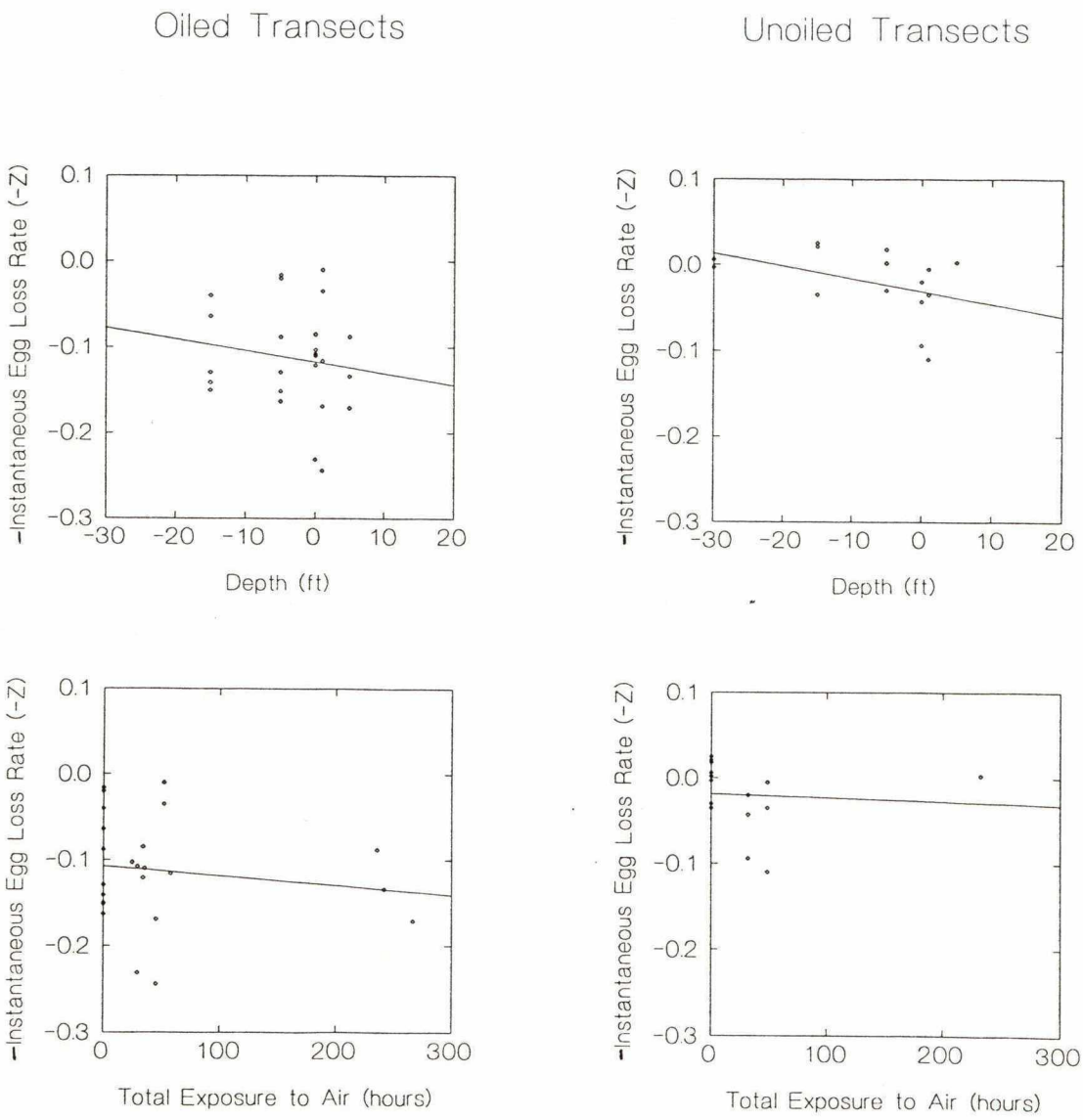


Figure 4. Egg loss rates for previously oiled and unoiled transects in 1990. Egg loss rates are plotted against both depth and air exposure.

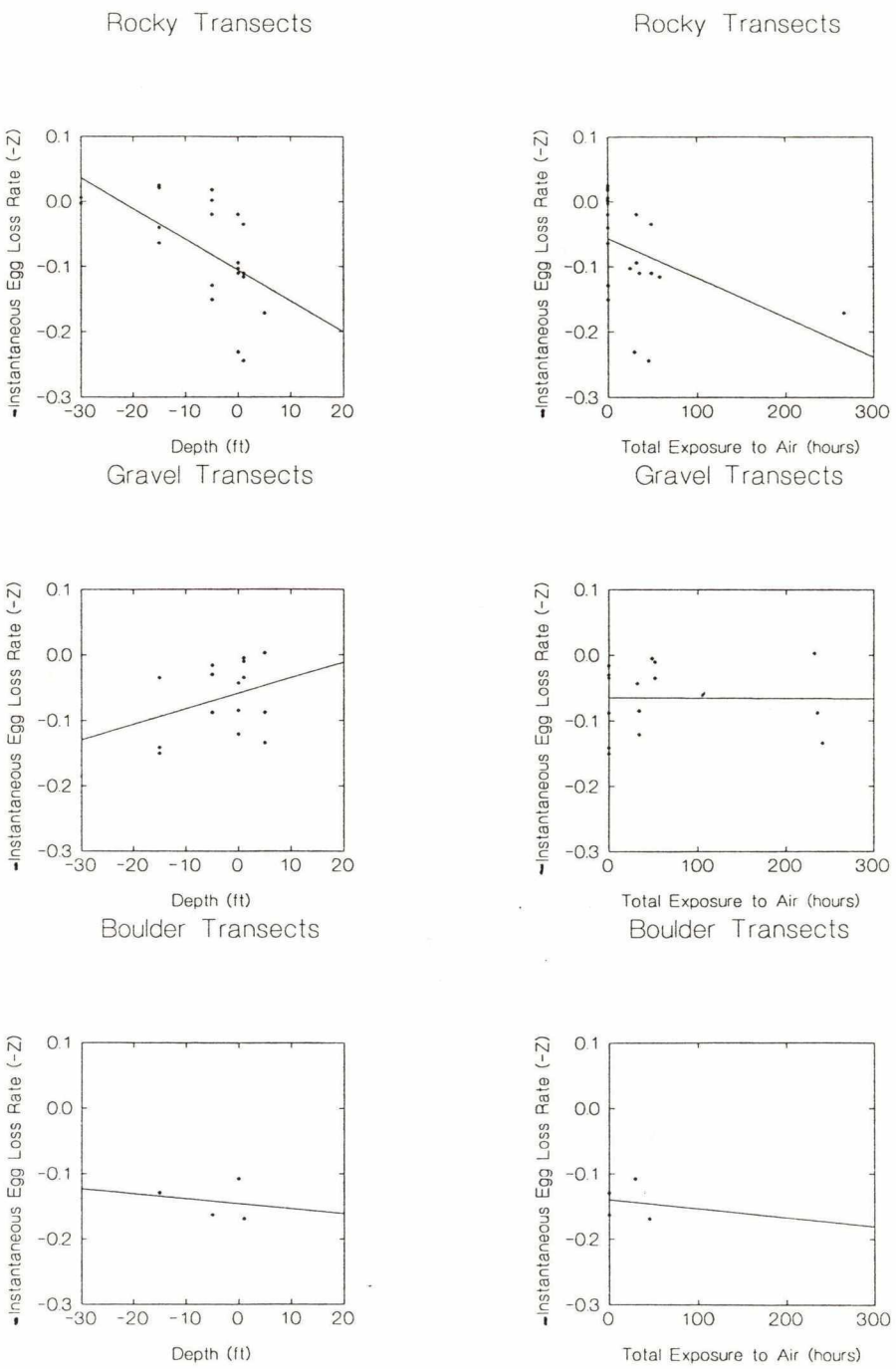


Figure 5. Egg loss rates for each substrate type sampled in 1990. Egg loss rates are plotted against both depth and air exposure.

includes data from five transects while both the gravel and boulder substrates have fewer data points, being represented by three and one transects respectively.

One of the problems with analyzing the kelp type variable is the absence of large brown kelp at the upper depths of herring spawn deposition. Patterns in egg loss rates between the two kelp type categories may be the result of the confounding effects of the variable with depth (Figure 6). The large brown kelp dominant category does not include depths above mean low water, while the large brown kelp non-dominant category has very few data points below mean low water.

Depth appeared to strongly influence egg abundance, with higher egg loss rates at the shallower depths (Figure 7). This pattern is evident when egg loss rates are plotted against air exposure as well.

Analysis of Covariance

Analysis of covariance techniques were used to evaluate the ln(egg abundance) data, with days since spawn as the covariate. Habitat variables used included depth, wave exposure, oiled/unoiled, kelp type and substrate type, as well as a number of interaction terms. Most terms in the ANCOVA were significant (Table 3). The habitat term explaining the most variability in the data set was the interaction between kelp type and oiled/unoiled condition. The analysis of covariance itself explained only 43.6% of the variability in ln(egg abundance).

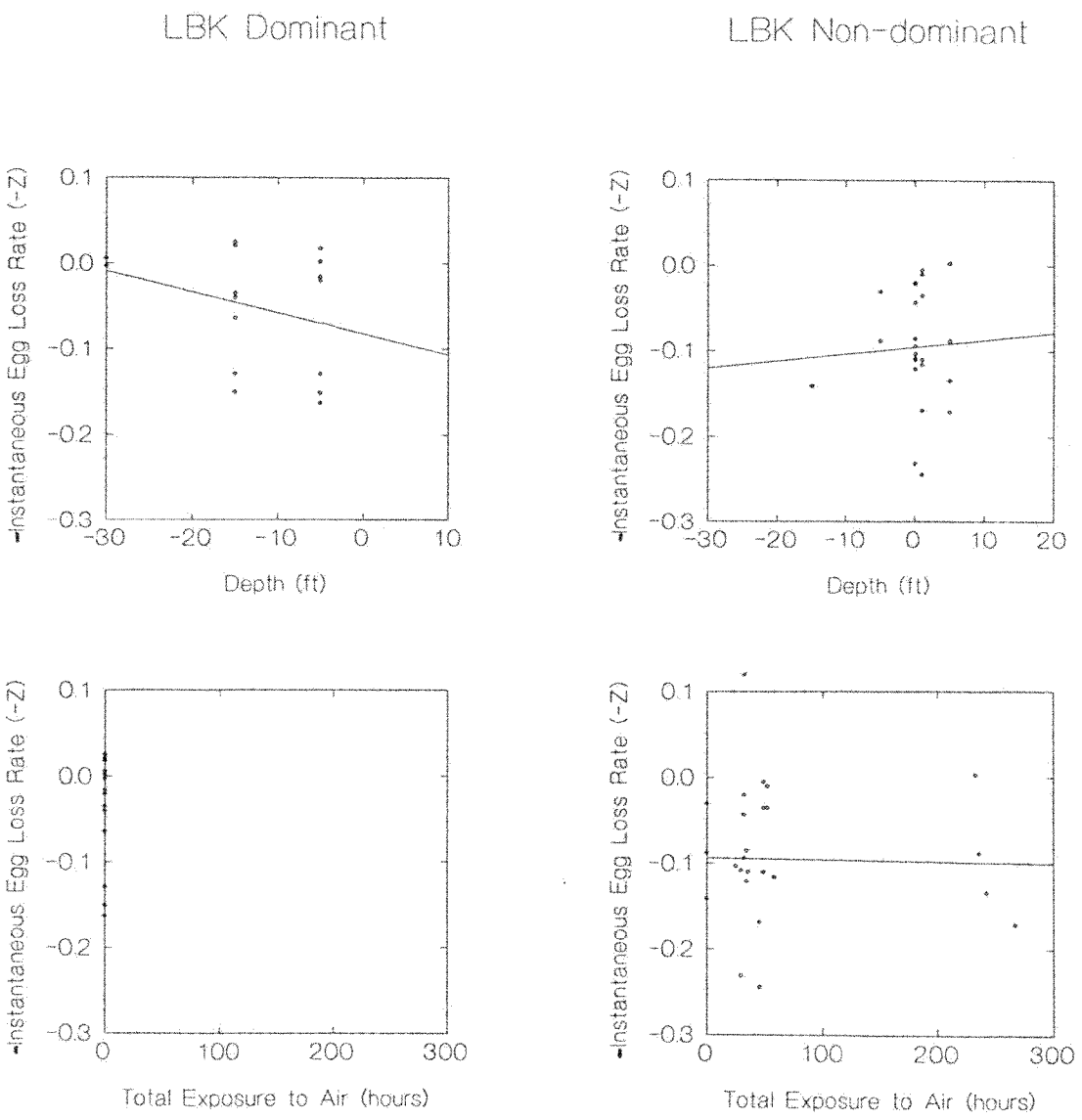


Figure 6. Egg loss rates in each kelp type category for 1990. LBK dominant are quadrats where large brown kelp (LBK) is the predominant kelp type, and LBK non-dominant are quadrats dominated by other kelp types. Egg loss rates are plotted against both depth and air exposure.

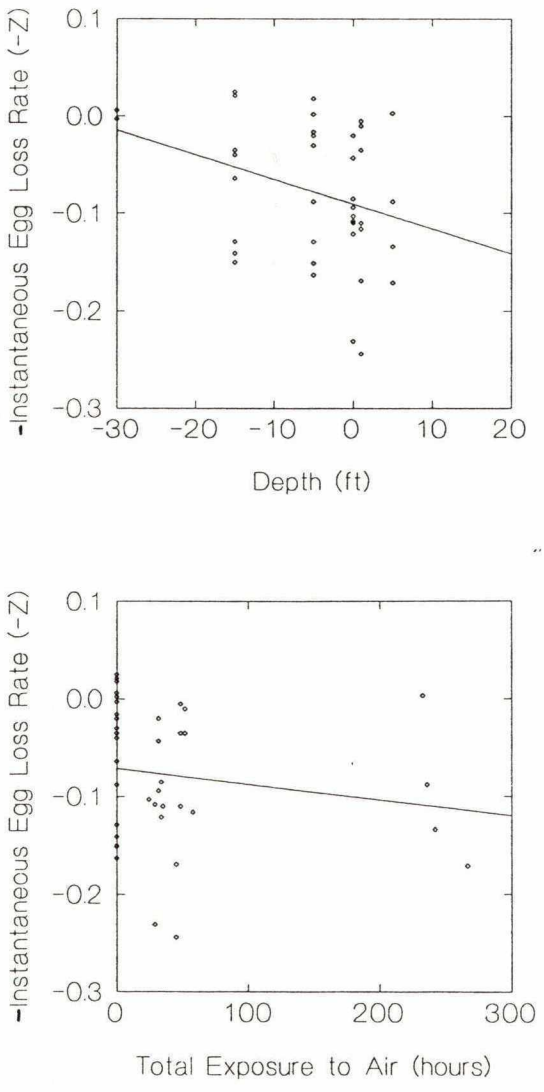


Figure 7. Egg loss rates against depth and air exposure in 1990.

Table 3. Results of analysis of covariance of 1990 ln(egg abundance) data. All habitat variables and all possible interaction terms are included in the analysis.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

N: 2239 Multiple R: 0.660 Squared Multiple R: 0.436

Source	Sum of Squares	DF	MS	F-Ratio	P
Oiled/Unoiled*Kelp type	281.781	1	281.781	121.058	0.000
Substrate type*Kelp type	36.579	2	18.289	7.857	0.000
Wave exposure*Kelp type	126.965	1	126.965	54.546	0.000
Wave exposure*days	3.812	1	3.812	1.638	0.201
Oiled/Unoiled*days	64.148	1	64.148	27.559	0.000
Substrate*days	22.989	2	11.495	4.938	0.007
Kelp type*days	5.146	1	5.146	2.211	0.137
Depth*days	29.095	5	5.819	2.500	0.029
Days since spawn	53.660	1	53.660	23.053	0.000
Kelp type	0.000	1	0.000	0.000	0.991
Oiled/unoiled	95.863	1	95.863	41.184	0.000
Wave exposure	159.067	1	159.067	63.338	0.000
Substrate	121.766	2	60.883	26.156	0.000
Depth	25.161	5	5.032	2.162	0.056
Error	5151.101	2213	2.328		

Factorial Analyses

Egg loss rates obtained from each transect at each depth in 1990 were dependent variables in analysis of variance models to determine habitat variables affecting egg loss. Because of the unbalanced sampling design in this year, a number of different data sets were modeled for egg loss rates in 1990. The data was grouped by substrate in three ways: all substrates, rocky and boulder substrates combined, and rocky substrates only. Because of the different depths sampled at some transects, models including only some of the depths were analyzed to maximize the interaction terms available for each model. Data sets with the -30 foot depth removed were modeled for all substrates as well as for rocky substrate only. Similarly data sets with both the -30 and +5 foot depths were modeled in both substrate groupings. Factorial analysis of data sets including air exposure over the incubation period in the place of depth was also performed in each of the substrate groupings. The complete set of models analyzed for the 1990 data are reported in Appendix A of Rooper et al. (1996).

The best model of 1990 egg loss rates contained data from all depths from transects on the rocky substrate. Factorial analysis resulted in a model explaining approximately 85.4% of the variability (Table 4), containing three terms; presence or absence of oil, wave exposure and depth.

Table 4. Results of factorial analysis of 1990 egg loss rates. This model explains the most variation in the 1990 data. Data used in this analysis is from the rocky substrate.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate (Z)

N: 21 Multiple R: 0.924 Squared Multiple R: 0.85

Source	Sum of Squares	DF	MSE	F-Ratio	P
Oiled/Unoiled	0.057	1	0.057	38.799	0.000
Wave exposure	0.016	1	0.016	11.058	0.005
Depth	0.042	5	0.008	5.698	0.005
Error	0.019	13	0.001		

Factorial analysis of the same data with air exposure in the place of depth leads to a model explaining 80.3% of the variability in egg loss rates (Table 5). The model also contains three terms; wave exposure, oiled/unoiled condition and kelp type.

The presence of the kelp type variable probably reflects the strength of depth in explaining egg loss rates. No large brown kelp dominated quadrats were located above mean low water, so the variables are confounded. Average egg loss rates in large brown kelp dominated quadrats was 0.030 (SE=0.018), while at quadrats dominated by other kelp types, egg loss rates averaged 0.123 (SE=0.023). The expected result was that large brown kelp would lead to higher egg loss, and since this was not observed, the observed effect may be that of depth. The average egg loss rate at oiled transects in 1990 was 0.125 (SE=0.022) while the average in unoiled transects was only 0.019 (SE=0.015). At wave-exposed transects, the average egg loss rate was 0.091 (SE=0.027), slightly higher than at wave-protected transects, 0.070 (SE=0.022).

1.3.2. 1991 Analysis

The 1991 data set included ln(egg abundance) estimates over time from six transects (Figure 1). Quadrats were placed at the same depths in 1991 as in 1990, with the exception of the -30 ft depth which was excluded in 1991. The only substrate sampled in 1991 was the rocky type substrate.

Table 5. Results of factorial analysis of 1990 egg loss rates with air exposure in the place of depth. Egg loss rates are from the rocky substrate only.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate,

N: 21 Multiple R: 0.896 Squared Multiple R: 0.803

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type	0.035	1	0.035	23.159	0.000
Wave exposure	0.014	1	0.014	8.923	0.008
Oiled/Unoiled	0.059	1	0.059	39.282	0.000
Error	0.026	17	0.002		

Graphical Analyses

Egg loss rates in 1991 ranged from 0.263 to -0.059 with an average of 0.042, and a standard error of 0.013 (Table 6, Figure 8). About 58% of the egg loss regressions were significant. Differences in egg loss rates between the wave-exposed and wave-protected categories were apparent when they were plotted against both depth and air exposure (Figure 9). Egg loss appeared to be slightly higher at wave-protected transects than at wave-exposed transects. As in the previous year, egg loss rates appeared to be higher at oiled transects than at unoiled transects in 1991 (Figure 10). This pattern was especially apparent when egg loss rates are plotted against air exposure.

When egg loss rates were plotted against depth in the two kelp type categories, no large differences were observed (Figure 11). No large brown kelp dominated quadrats were ever exposed to air during incubation, since no quadrats above mean low water were dominated by large brown kelp.

The remaining variable in 1991 is depth. There appeared to be a general trend of higher egg loss rates at higher depths, which is consistent with the 1990 results (Figure 12).

Analysis of Covariance

Analysis of covariance was performed on the 1991 ln(egg abundance) data using days as the covariate. The habitat variables available for this analysis included depth, wave exposure, oiled/unoiled and a number of interaction terms. Most of the terms were

Table 6. Summary of 1991 egg loss regressions from each transect by depth. R=rocky, P=wave-protected, E=wave-exposed, O=oiled area, and C=unoiled area.

Depth (ft)	**Transect** Habitat classification	**26** O,E,R	**28** O,E,R	**12** C,P,R	**15** C,P,R	**21** C,P,R	**25** C,P,R
5	slope (-Z)		-0.036	-0.074		-0.263	
	intercept		4.430	4.303		6.155	
	R^2		0.098	0.753		0.828	
	p-value		0.060	0.000		0.000	
1	slope (-Z)	0.006	0.030	-0.058	-0.026	-0.098	-0.132
	intercept	4.619	5.070	5.330	3.026	4.374	5.179
	R^2	0.002	0.172	0.300	0.087	0.436	0.189
	p-value	0.792	0.013	0.005	0.152	0.002	0.030
0	slope (-Z)	-0.004	0.059	-0.028	-0.093	-0.112	-0.047
	intercept	4.555	4.315	6.142	5.127	5.325	3.682
	R^2	0.001	0.436	0.173	0.590	0.583	0.014
	p-value	0.865	0.000	0.039	0.000	0.000	0.580
-5	slope (-Z)	-0.006	0.039	-0.035	-0.043	-0.017	-0.026
	intercept	4.639	3.396	6.253	4.553	4.679	3.336
	R^2	0.002	0.142	0.240	0.352	0.021	0.017
	p-value	0.820	0.025	0.013	0.000	0.487	0.580
-15	slope (-Z)	0.057	0.019	-0.112	-0.051	-0.044	
	intercept	0.949	4.842	5.439	4.722	4.186	
	R^2	0.166	0.030	0.370	0.275	0.121	
	p-value	0.039	0.320	0.001	0.002	0.088	

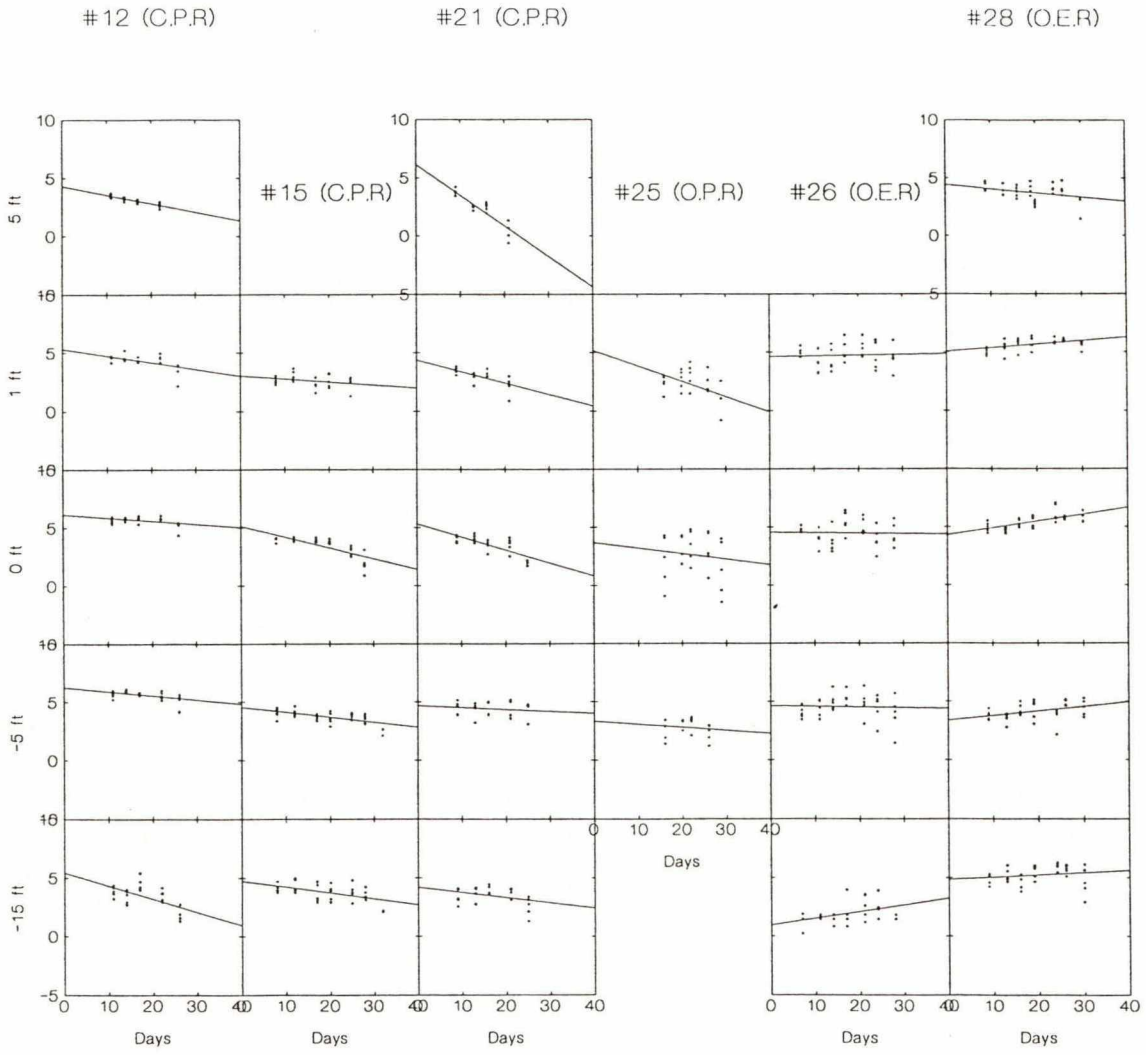


Figure 8. Regressions of ln(egg abundance) against days since spawn for 1991 transects. The estimate of the egg loss rate (Z) at each depth is represented by the straight line in each graph. C=unoiled, O=oiled, R=rocky substrate, P=wave-protected, and E=wave-exposed.

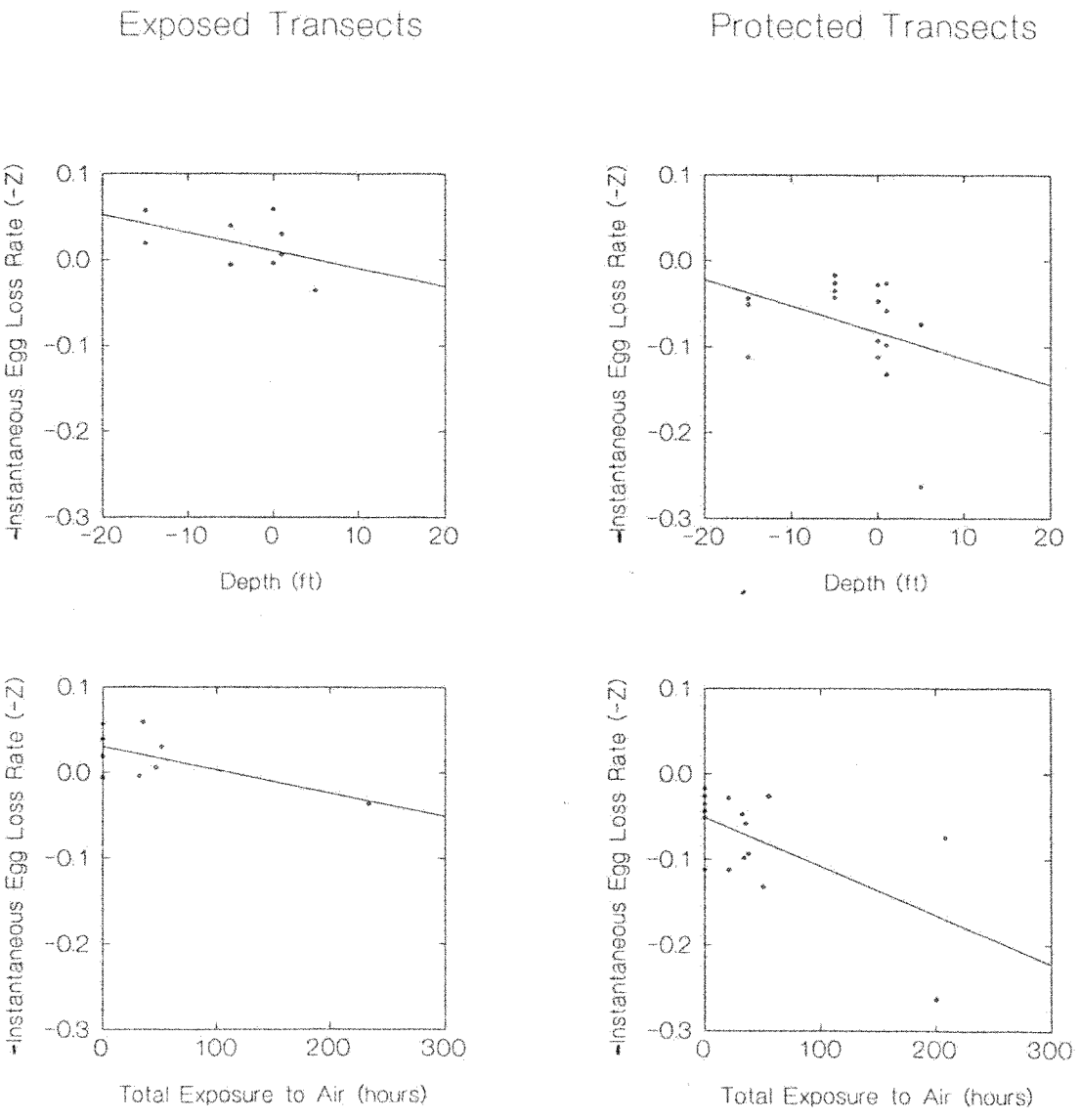


Figure 9. Egg loss rates for wave-exposed and wave-protected transects in 1991. Egg loss rates are plotted against both depth and air exposure.

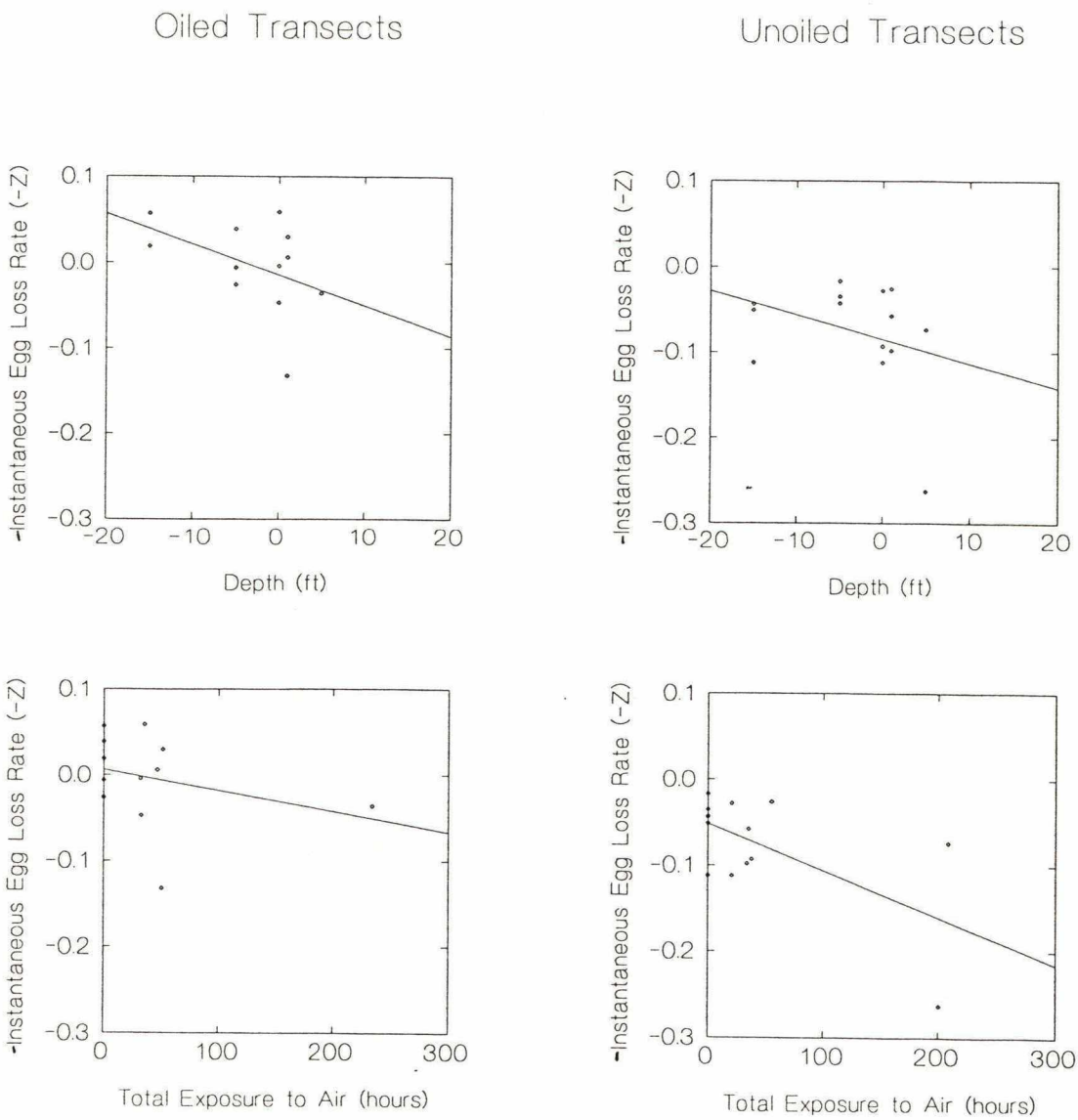


Figure 10. Egg loss rates for previously oiled and unoiled transects in 1991. Egg loss rates are plotted against both depth and air exposure.

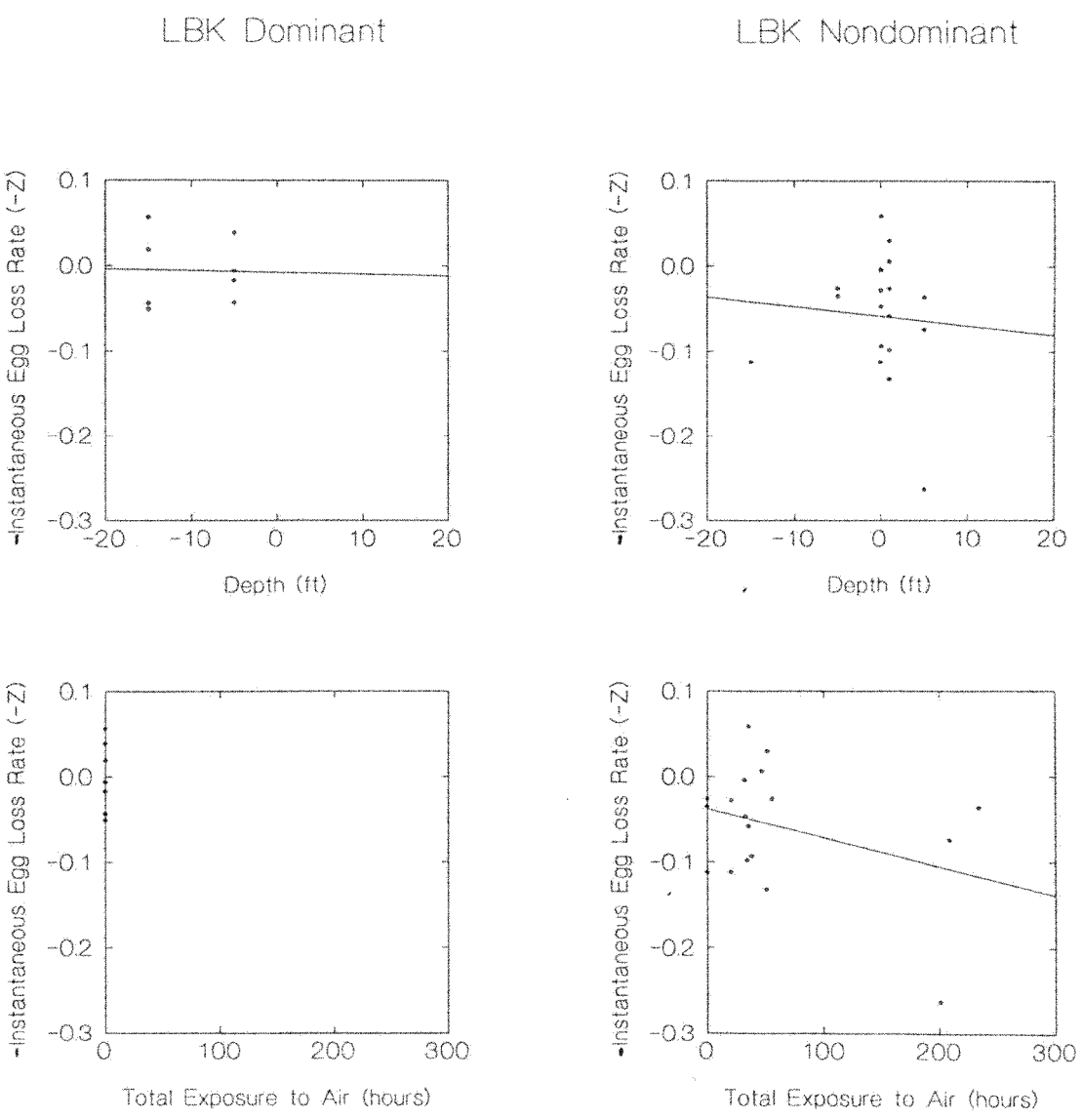


Figure 11. Egg loss rates in each kelp type category for 1991. LBK dominant refers to quadrats dominated by large brown kelp (LBK) and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted against both depth and air exposure.

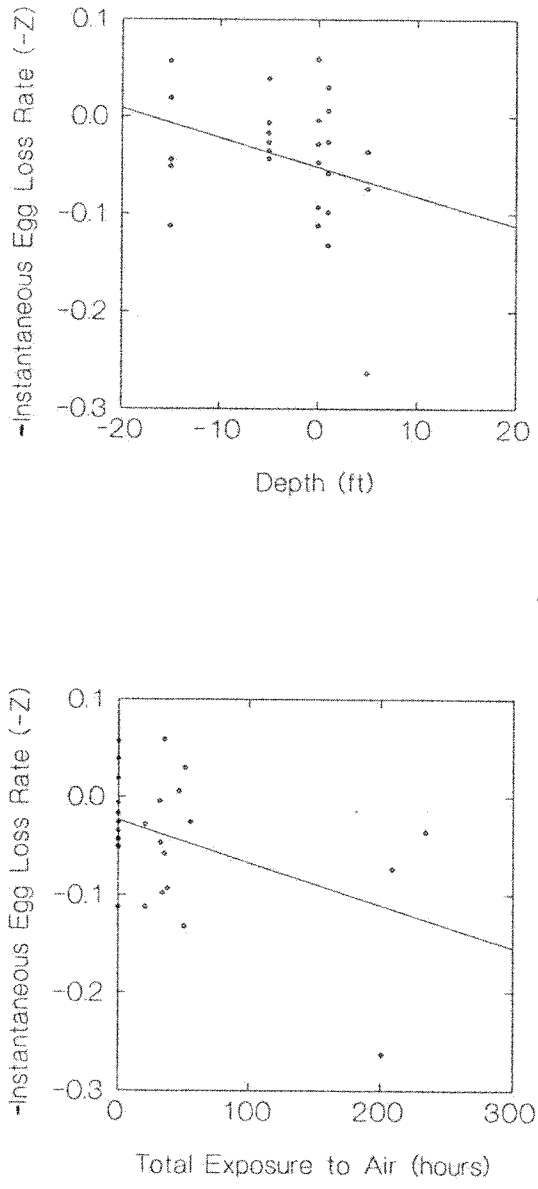


Figure 12. Egg loss rates against depth and air exposure in 1991.

insignificant except the wave exposure*depth, wave exposure*(days since spawn), and the depth*(days since spawn) interaction, as well as the depth and (days since spawn) terms (Table 7). The analysis of covariance explained 41.1% of the variability in ln(egg abundance) with the wave exposure*depth interaction term the most significant of the habitat variables.

Factorial Analyses

As in 1990, multiple models of the 1991 egg loss rates were examined. Three models of the 1991 data were analyzed and compared: a model of all the 1991 data, a model of all the 1991 data with air exposure in the place of depth, and a subset of the 1991 data excluding the +5 foot depth. The best model in 1991 explained 65.3% of the variability in egg loss rates and contained two significant habitat variables, depth and wave exposure (Table 8).

A similar model resulted from replacing depth with air exposure. The significant variables in this model were: air exposure and wave exposure. The model explains 62.8% of the total variability in egg loss rates in 1991 (Table 9).

At wave-protected transects the average egg loss rate (Z) was 0.074 (SE=0.015), while at wave-exposed transects the average was -0.018 (SE=0.010). Egg loss rates were inversely related to depth and air exposure: higher egg loss rates occurred at shallower depths, and at longer times of air exposure (Figure 12).

Table 7. Results of analysis of covariance of 1991 ln(egg abundance) data. All habitat variables and all possible interaction terms are included.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

N: 730 Multiple R: 0.641 Squared Multiple R: 0.4

Source	Sum of Squares	DF	MSE	F-Ratio	P
Wave exposure*Depth	50.245	4	12.561	11.069	0.000
Wave exposure*Kelp type	0.048	1	0.048	0.042	0.837
Wave exposure*Days	12.032	1	12.032	10.603	0.001
Oiled/unoiled*Days	0.115	1	0.115	0.101	0.751
Kelp type*Days	0.031	1	0.031	0.027	0.870
Depth*Days	14.997	4	3.749	3.304	0.011
Wave exposure	0.202	1	0.202	0.178	0.673
Oiled/Unoiled	2.591	1	2.591	2.283	0.131
Kelp type	1.207	1	1.207	1.063	0.303
Depth	12.022	4	3.006	2.648	0.032
Days since spawn	11.695	1	11.695	10.306	0.001
Error	804.605	709	1.135		

Table 8. Results of factorial analysis of 1991 egg loss rates. This model explains the most variability in the 1991 data.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate,

N: 26 Multiple R: 0.808 Squared Multiple R: 0.653

Source	Sum of Squares	DF	MSE	F-Ratio	P
Depth	0.025	4	0.006	3.168	0.036
Wave exposure	0.049	1	0.049	24.516	0.000
Error	0.040	20	0.002		

Table 9. Results of factorial analysis of 1991 egg loss rates with air exposure in the place of depth.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 26 Multiple R: 0.792 Squared Multiple R: 0.628

Source	Sum of Squares	DF	MSE	F-Ratio	P
Air exposure	0.023	1	0.023	12.050	0.002
Wave exposure	0.052	1	0.052	27.617	0.000
Error	0.043	23	0.002		

1.3.3. 1994 Analyses

Egg loss sampling in 1994 was carried out at 10 transects located between Rocky Bay and Port Chalmers on Montague Island (Figure 1). Four transects located on boulder substrate and three transects on rocky substrate were classified as wave-exposed, while the remaining three transects were classified as wave-protected. Of the remaining transects, one was located on mud substrate and the other two on a sandy substrate. Quadrats sampled over the incubation period were placed at three different depths at each transect, ranging from -10 feet to +3 feet (Table 1). All of the transects had quadrats at the lowest depth; however, the other two depths varied depending on the location of spawn. This resulted in an unbalanced design for most variables within transects as well as on a transect by transect basis. Since the same depths were not replicated at each transect and the substrate variable was confounded with the wave exposure variable, several different subsets of the egg loss data were examined, resulting in a number of different egg loss models.

Graphical Analyses

The average egg loss rate (Z) was 0.096 with a standard error of 0.012 in 1994. The range of egg loss rates was from 0.242 to -0.112, and about 90% of the egg loss regressions were statistically significant (Table 10, Figure 13).

Table 10. Summary of 1994 egg loss regressions from each transect by depth. Depths with no replicates are included in their nearest neighboring category. R=rocky, B=boulder, M=mud, S=sand, P=wave-protected, E=wave-exposed.

Depth (ft)	Transect / Habitat classification	4 B,E	7 B,E	8 B,E	9 B,E	1 R,E	5 R,E	6 R,E	2 M,P	3 S,P	10 S,P
3	slope (-Z)	-0.192			-0.100	-0.222	-0.125				
	intercept	6.483			5.180	6.125	5.975				
	R^2	0.767			0.474	0.768	0.520				
	p-value	0.000			0.000	0.000	0.000				
2	slope (-Z)		-0.156	-0.071				-0.135			
	intercept		6.431	5.512				7.272			
	R^2		0.566	0.502				0.770			
	p-value		0.000	0.000				0.000			
0	slope (-Z)								-0.063	-0.242	0.112
	intercept								6.282	4.325	0.970
	R^2								0.688	0.645	0.231
	p-value								0.000	0.000	0.003
-2	slope (-Z)								-0.014		-0.101
	intercept								3.180		6.720
	R^2								0.010		0.562
	p-value								0.511		0.000
-3	slope (-Z)	-0.086	-0.093	-0.035	-0.092	-0.096	-0.115	-0.055		-0.146	
	intercept	5.813	7.988	5.162	6.436	6.435	5.653	7.059		6.287	
	R^2	0.050	0.693	0.275	0.409	0.430	0.111	0.227		0.668	
	p-value	0.282	0.000	0.001	0.000	0.000	0.067	0.008		0.000	
-10	slope (-Z)	-0.081	-0.099	-0.102	-0.077	-0.060	-0.107	-0.110	-0.125	-0.063	-0.033
	intercept	4.255	6.066	5.362	3.861	5.000	4.830	7.196	5.758	5.199	3.459
	R^2	0.232	0.463	0.475	0.182	0.128	0.457	0.428	0.309	0.293	0.259
	p-value	0.017	0.000	0.000	0.010	0.035	0.000	0.000	0.004	0.000	0.002

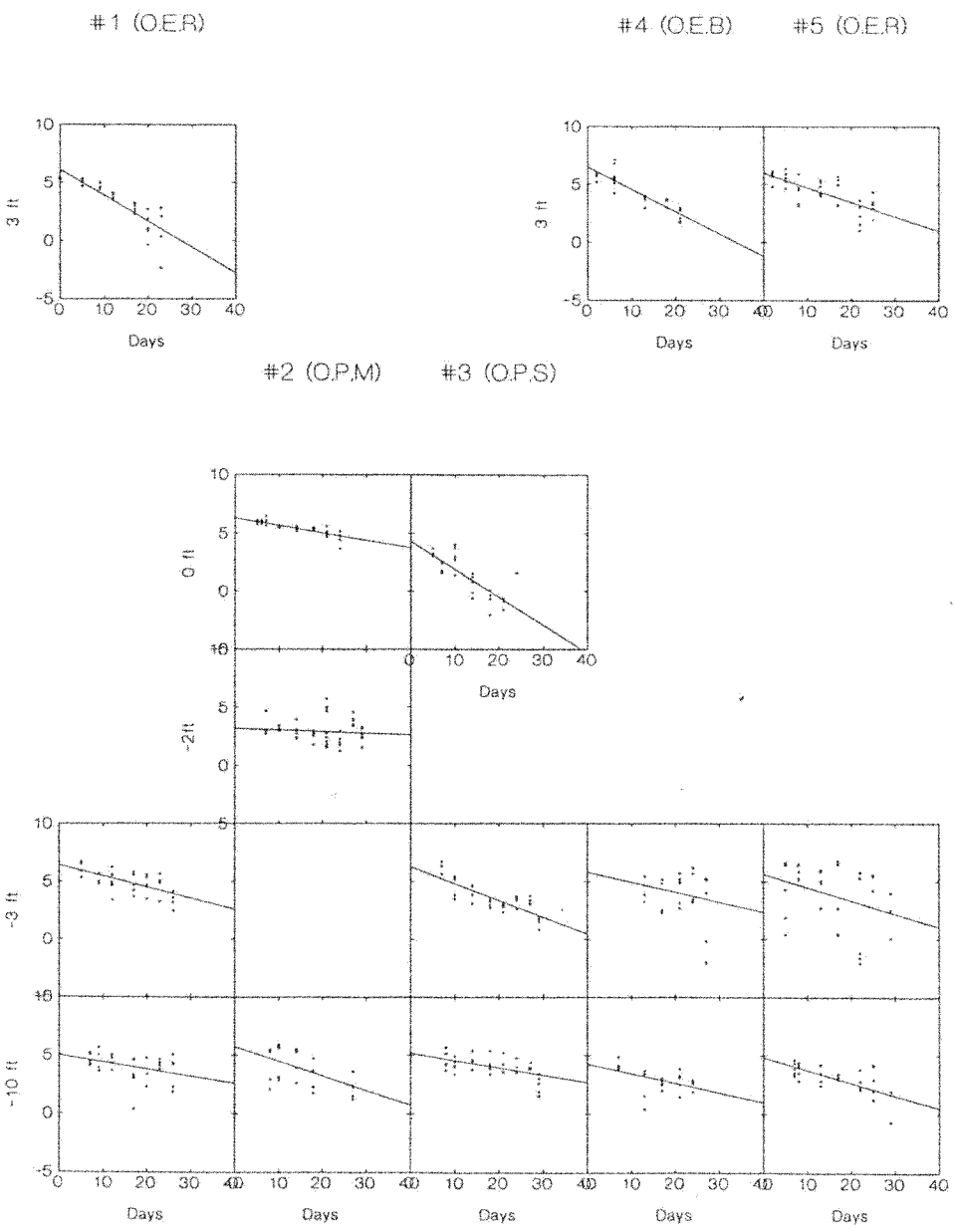


Figure 13. Regressions of ln(egg abundance) against days since spawn for 1994 transects. In each graph the line represents the best estimate of the egg loss rate (Z) at each depth. C=unoiled, O=oiled, R=rocky substrate, M=mud substrate, S=sand substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.

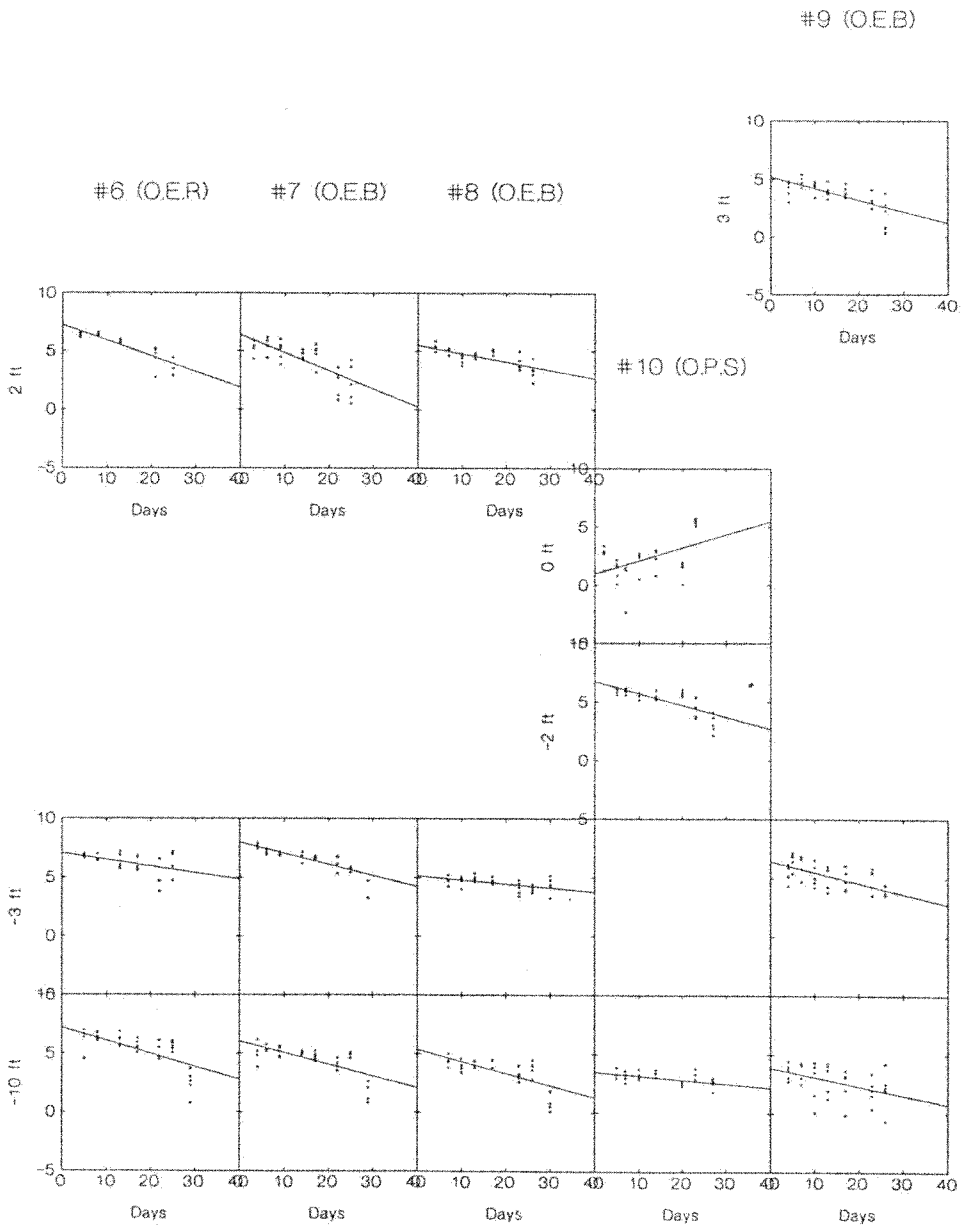


Figure 13 (continued). Regressions of ln(egg abundance) against days since spawn for 1994 transects. In each graph the line represents the best estimate of the egg loss rate (Z) at each depth. C=unoiled, O=oiled, R=rocky substrate, M=mud substrate, S=sand substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.

Graphical analysis of data in the wave-exposed and the wave-protected categories revealed that egg loss rates did not vary much between the two conditions in 1994 when plotted against both depth and air exposure (Figure 14).

Egg loss rates in each of the substrate types were also plotted against both depth and air exposure (Figure 15). In these plots it is evident that egg loss did not differ much between rocky and boulder substrates. However, the sand and mud substrates did seem to exhibit differences in egg loss rates. These two substrates were represented by far fewer data points which may explain the observed patterns.

Graphical analysis of kelp type revealed that, except at the lower depths, there were not many data points for the large brown kelp dominated category (Figure 16). So even though the two categories seem to exhibit a high degree of difference in egg loss, it is unclear if this is caused by kelp effects, depth effects, or sample size effects.

Egg loss rates at each depth were also examined, as well as egg loss rates against air exposure (Figure 17). As in previous years, egg loss rates appear to be inversely related to both depth and air exposure.

Egg loss rates were then plotted against the covariate, cumulative loose eggs (Figure 18), and the two bird covariates, average glaucous winged gull abundance and average bird abundance (Figure 19 and Figure 20). Egg loss rates seem to increase with all covariates: at higher bird and gull abundance egg loss rates are higher, and at transects with higher loose egg counts, egg loss rates are higher.

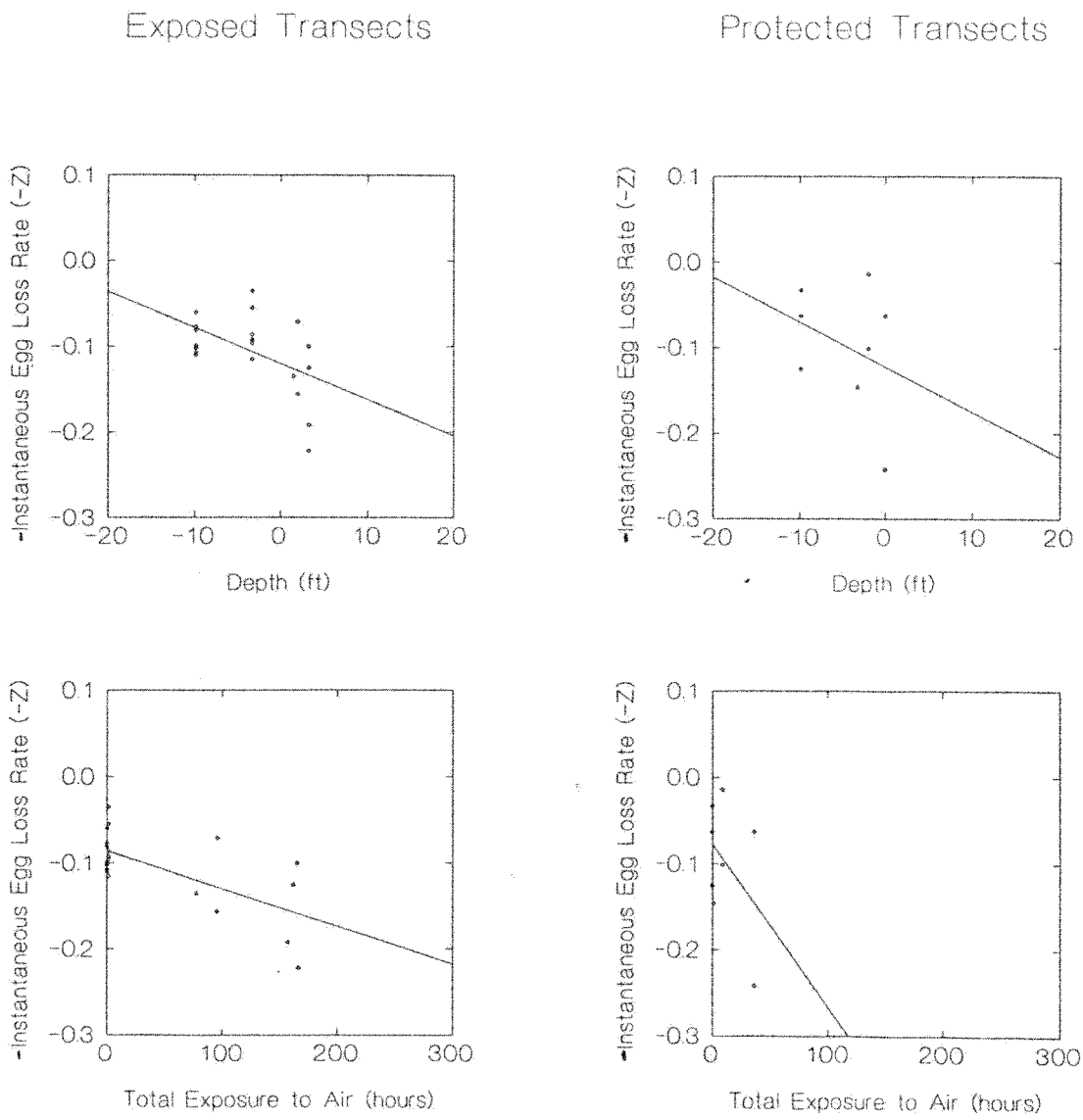


Figure 14. Egg loss rates for wave-exposed and wave-protected transects in 1994. Egg loss rates are plotted against both depth and air exposure.

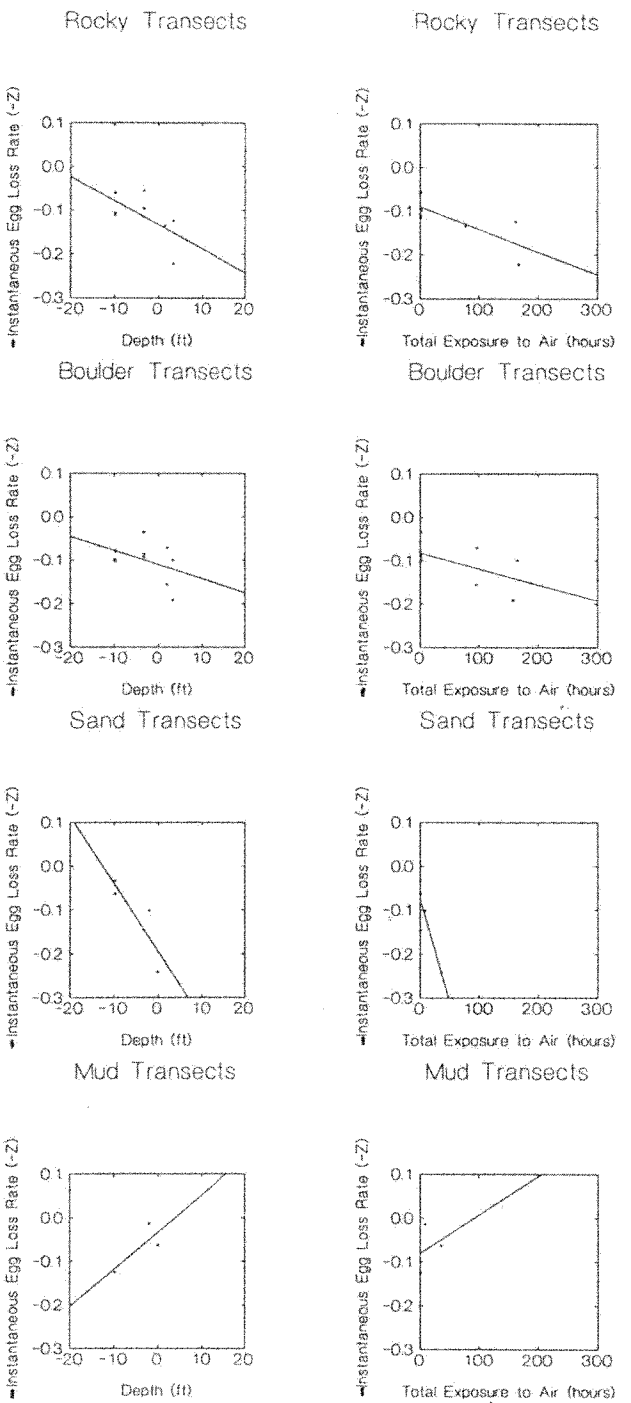


Figure 15. Egg loss rates for each substrate type sampled in 1994. Egg loss rates are plotted against both depth and air exposure.

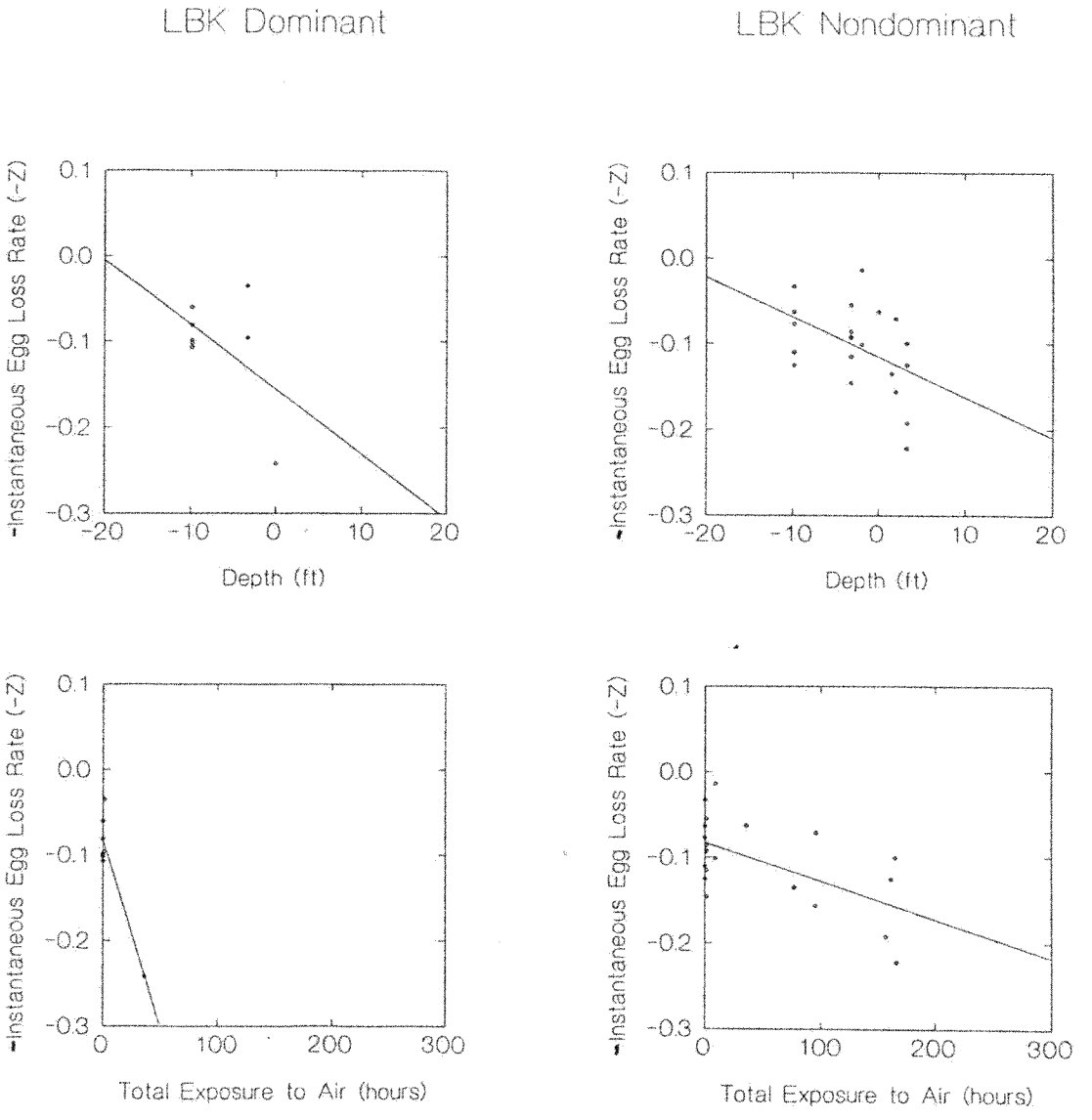


Figure 16. Egg loss rates for each kelp type category in 1994. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK) species, and LBK non-dominant refers to quadrats inhabited by other vegetation types. Egg loss rates are plotted against both depth and air exposure.

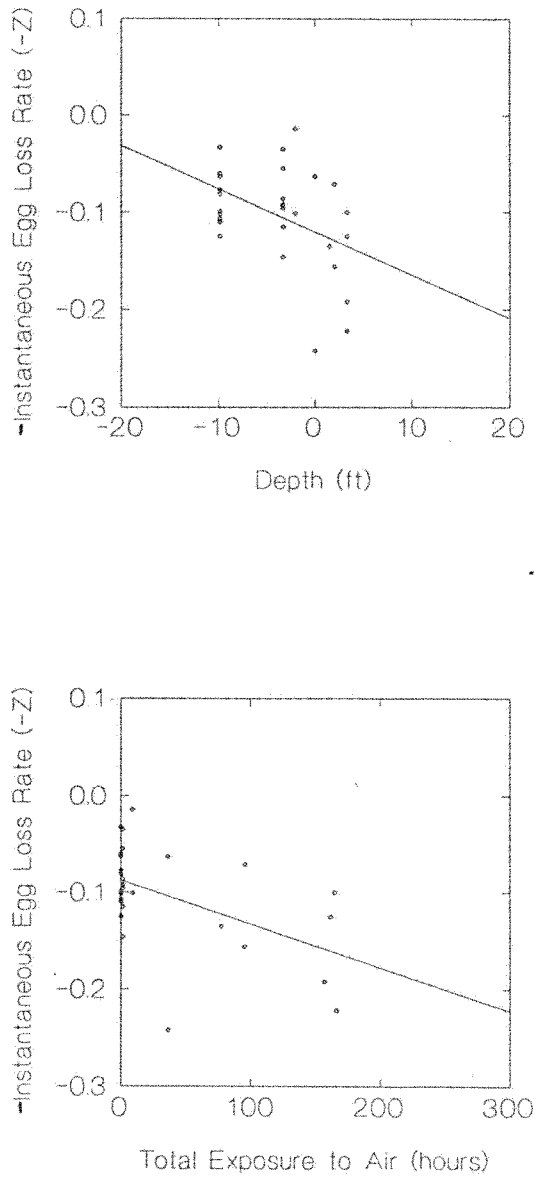


Figure 17. Egg loss rates against depth and air exposure in 1994.

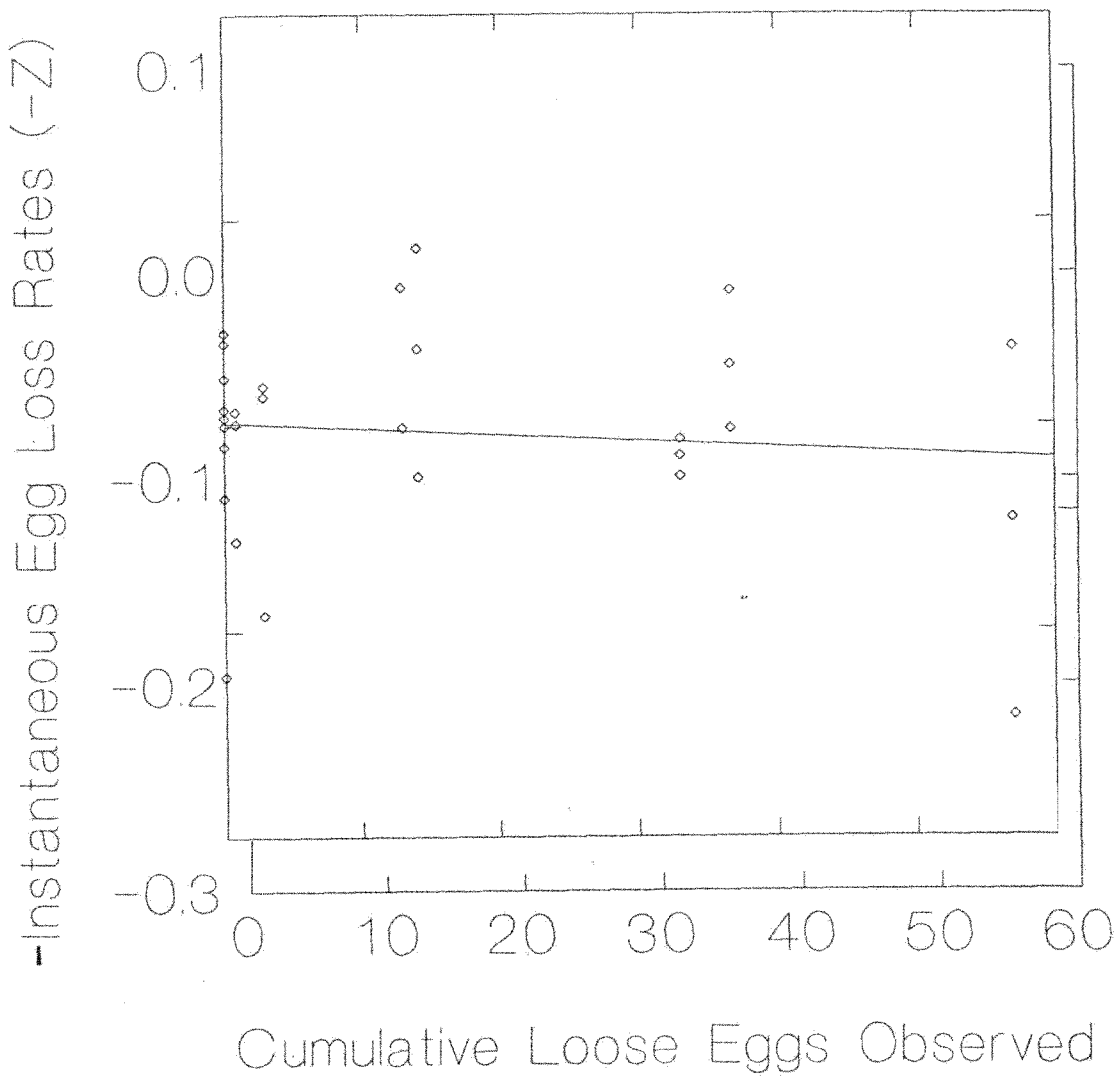


Figure 18. Egg loss rates against loose eggs observed at transects in 1994.

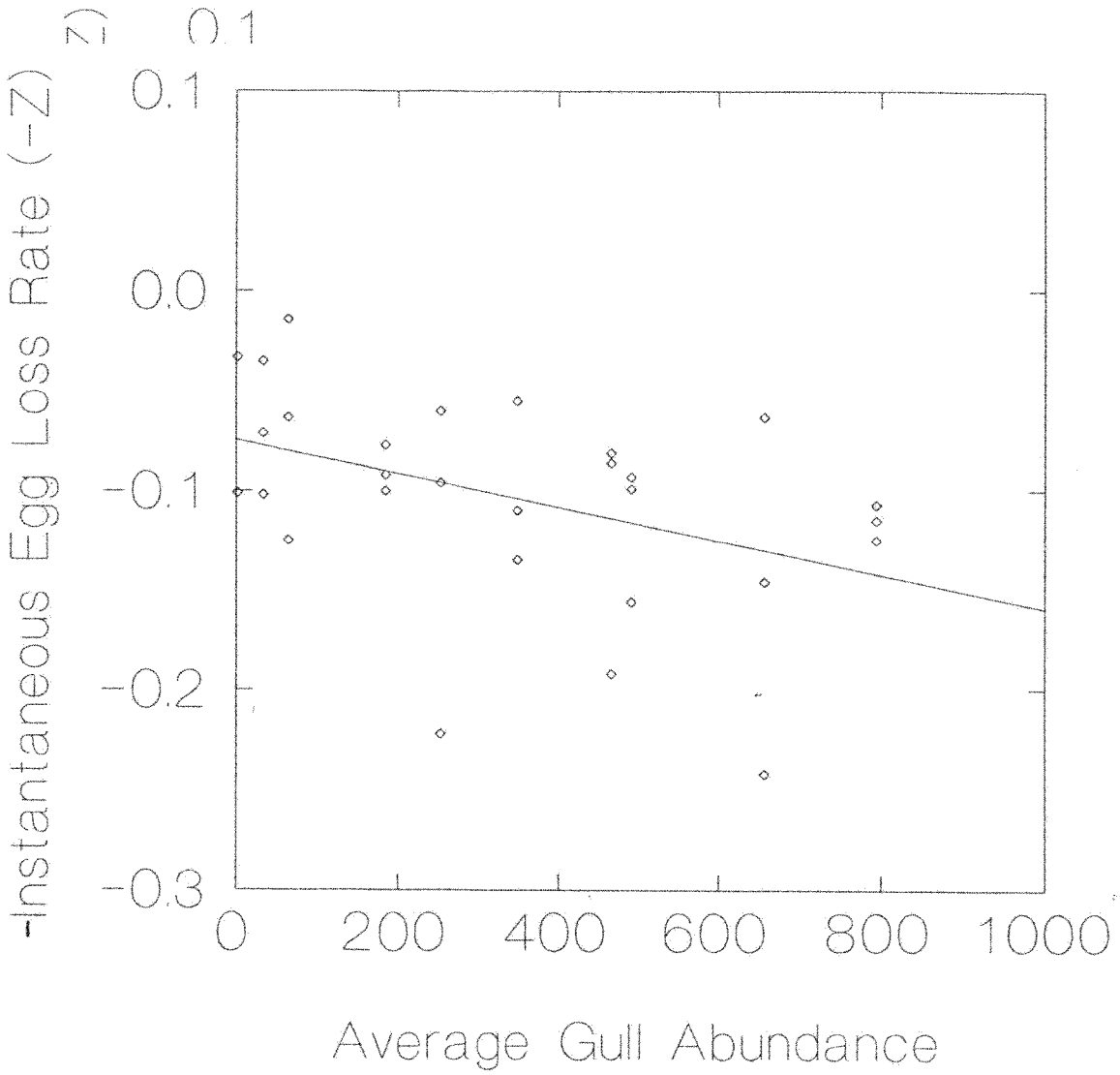


Figure 19. Egg loss rates against average glaucous winged gull abundance at 1994 transects.

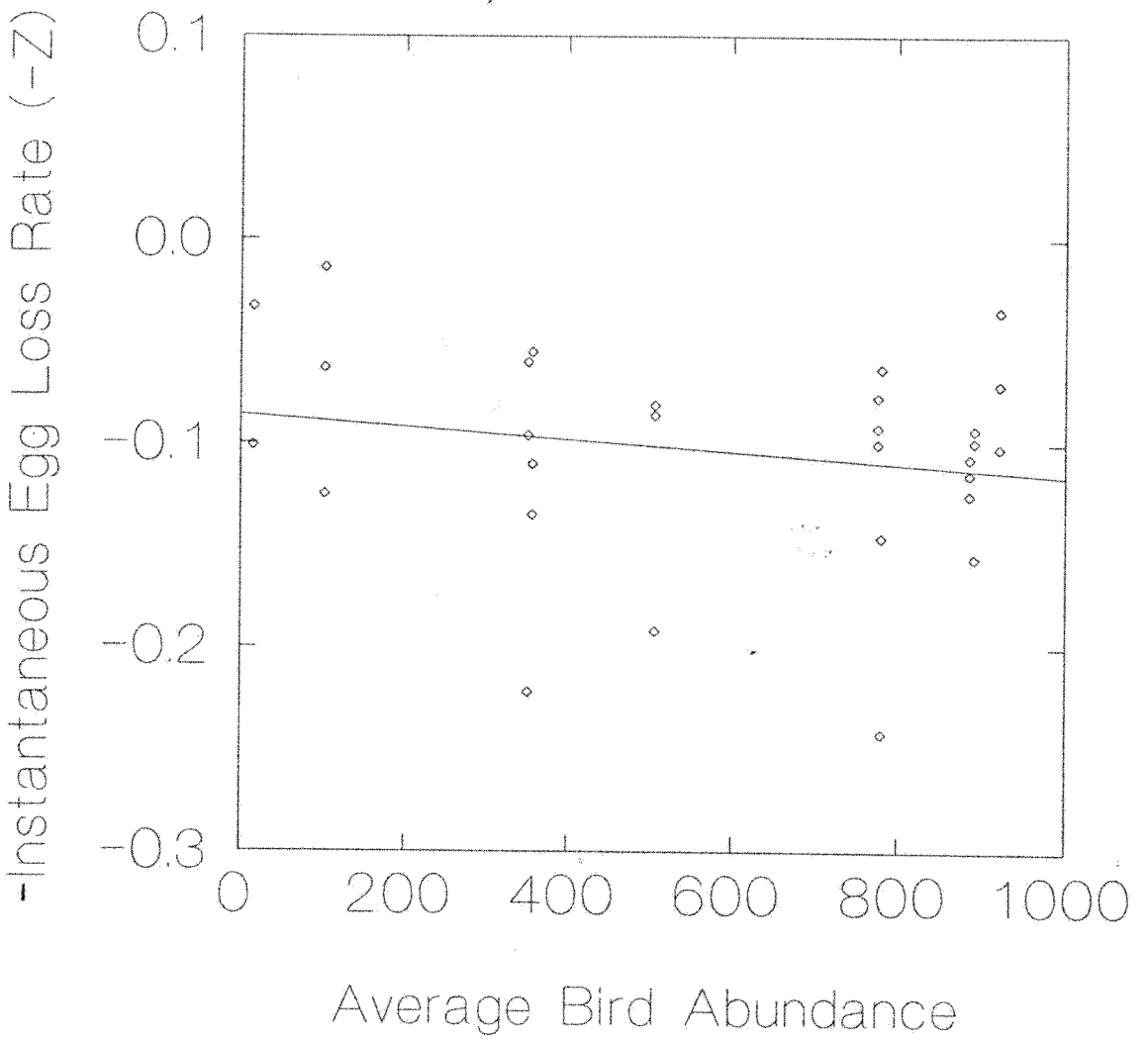


Figure 20. Egg loss rates against average number of birds observed at 1994 transects.

Analyses of Covariance

I performed two analyses of covariance on the raw data from 1994 with ln(egg abundance) as the dependent variable and (days since spawn) as the covariate. Two factors included in the ANCOVA were kelp type and depth relative to mean low water. Because of the unbalanced design, substrate and wave exposure were confounded, so one ANCOVA was run with substrate as a factor without wave exposure, and one ANCOVA excluding substrate with the wave exposure variable.

The results of the analyses with the substrate variable included yield a model explaining 40.6% of the variability in ln(egg abundance) data (Table 11). All of the factors, interaction terms and the covariate were significant in the analysis, with the covariate explaining the most variation in the data. When the wave exposure variable was included instead of substrate a model explaining 37.7% of the variability resulted (Table 12). Again, the covariate, days since spawn, accounted for the most variability in the data set, and most of the terms included in the model were significant.

Factorial Analyses

Because sampling at some depths was not repeated at more than one transect, a number of different categorizing strategies were used to obtain replication for the depth variable. The data were modeled for each of the strategies to determine the best method for handling the lack of replication for the depth variable. To maximize the number of replicates at each depth, one technique was to divide the depths into three fairly arbitrary

Table 11. Results of analysis of covariance of 1994 ln(egg abundance) data, without the wave exposure variable.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

N: 1024 Multiple R: 0.637 Squared Multiple R: 0.406

Source	Sum of Squares	DF	MSE	F-Ratio	P
Substrate type*Kelp type	24.624	3	8.208	4.527	0.004
Substrate type*Days	24.118	3	8.039	4.434	0.004
Kelp type*Days	7.655	1	7.655	4.222	0.040
Depth*Days	53.002	5	10.600	5.846	0.000
Substrate type	44.133	3	14.711	8.113	0.000
Kelp type	12.695	1	12.695	7.002	0.008
Depth	87.980	5	17.596	9.705	0.000
Days since spawn	265.462	1	265.462	146.407	0.000
Error	1814.990	1001	1.813		

Table 12. Results of analysis of covariance of 1994 ln(egg abundance) data, without the substrate type variable.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

N: 1024 Multiple R: 0.614 Squared Multiple R: 0.37

Source	Sum of Squares	DF	MSE	F-Ratio	P
Wave exposure*Kelp type	17.483	1	17.483	9.261	0.002
Wave exposure*Days	0.789	1	0.789	0.418	0.518
Kelp type*Days	6.396	1	6.396	3.388	0.066
Depth*Days	50.109	5	10.022	5.309	0.000
Wave exposure	24.392	1	24.392	12.922	0.000
Kelp type	21.783	1	21.783	11.540	0.001
Depth	73.902	5	14.780	7.830	0.000
Days since spawn	545.587	1	545.587	280.449	0.000
Error	1900.884	1007	1.888		

categories: d > 1 ft, 1 ft> d > -3 ft and d < -3 ft to maximize the number of replicates at each depth. The next technique used for categorizing depths was to group them with their closest linear category from the 1990 and 1991 depths. Another was to place them in corresponding 1990 and 1991 categories based on the amount of air exposure received throughout the incubation period. The best technique based on the results of modeling was to group the two depths with only one egg loss rate apiece with their closest possible depth. All the models were run for data combined over all substrates and for data in the rocky and boulder substrates only; these models are reported in Appendix A of Rooper et al. (1996).

The best model for the 1994 data explained 87.7% of the variability in egg loss rates (Table 13). The model contains egg loss rates combined over all substrates, and the two depths with single observations combined with their closest depth. The model contains two significant interaction terms, depth*bird abundance and wave exposure*kelp type. The habitat variables; wave exposure, depth, kelp type, and average gull abundance were also significant. Depth explains the most variation in egg loss rates for this model.

The significance of kelp type in the model is probably a byproduct of the extremely high significance of depth. Since large brown kelp dominated at depths below 0 ft, there is a slight confounding between the two variables. This makes it unclear which effect is being observed, the effect of depth or the effect of kelp type.

With the exclusion of kelp type from the factorial analysis, the best model for the 1994 data explained 73.6% of the variability in egg loss rates and contained only two terms,

Table 13. Results of factorial analysis of 1994 egg loss rates.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate,

N: 30 Multiple R: 0.936 Squared Multiple R: 0.87

Source	Sum of Squares	DF	MSE	F-Ratio	P
Depth*Average bird abundance	0.029	5	0.006	5.950	0.003
Wave exposure*Kelp type	0.013	1	0.013	12.865	0.003
Wave exposure	0.012	1	0.012	12.291	0.003
Kelp type	0.013	1	0.013	13.055	0.003
Depth	0.051	5	0.010	10.296	0.000
Average gull abundance	0.005	1	0.005	4.957	0.042
Error	0.015	15	0.001		

depth and the depth*average bird abundance interaction, with depth explaining the majority of the variation (Table 14). The 1994 data plotted by depth show that egg loss rates decrease at deeper depths (Figure 17), and that higher bird abundances led to higher egg loss rates (Figure 20).

1.3.4. 1995 Analyses

In 1995 eight egg loss transects were monitored over the incubation period. The transects were again located between Rocky Bay and Port Chalmers on Montague Island, since the major concentration of spawning herring occurred between these two inlets (Figure 1). Six of the eight transects were placed in rocky areas, and of these two were wave-protected and four were wave-exposed. The two other transects were located on gravel, did not include all the depths, and did not have many data points, so they were not used in the analyses. At each transect, quadrat frames were placed at six standard depths relative to mean low water, +5 ft, +3 ft, +1 ft, 0 ft, -1 ft, and -5 ft (Table 1).

Graphical Analyses

Ln(egg abundance) changes over time at each depth at each egg loss transect were used to compute the egg loss rate (Z) using linear regression (Figure 21). About 66% of the egg loss regressions were significant (Table 15). The average egg loss rate in 1995 was 0.096 with a standard error of 0.011. Egg loss rates ranged from 0.231 to -0.007.

Table 14. Results of factorial analysis of 1994 egg loss rates, excluding the kelp type variable from the analysis.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 30 Multiple R: 0.858 Squared Multiple R: 0.736

Source	Sum of Squares	DF	MSE	F-Ratio	P
Depth*Bird abundance	0.063	5	0.013	7.554	0.000
Depth	0.047	5	0.009	5.623	0.002
Error	0.032	19	0.001		

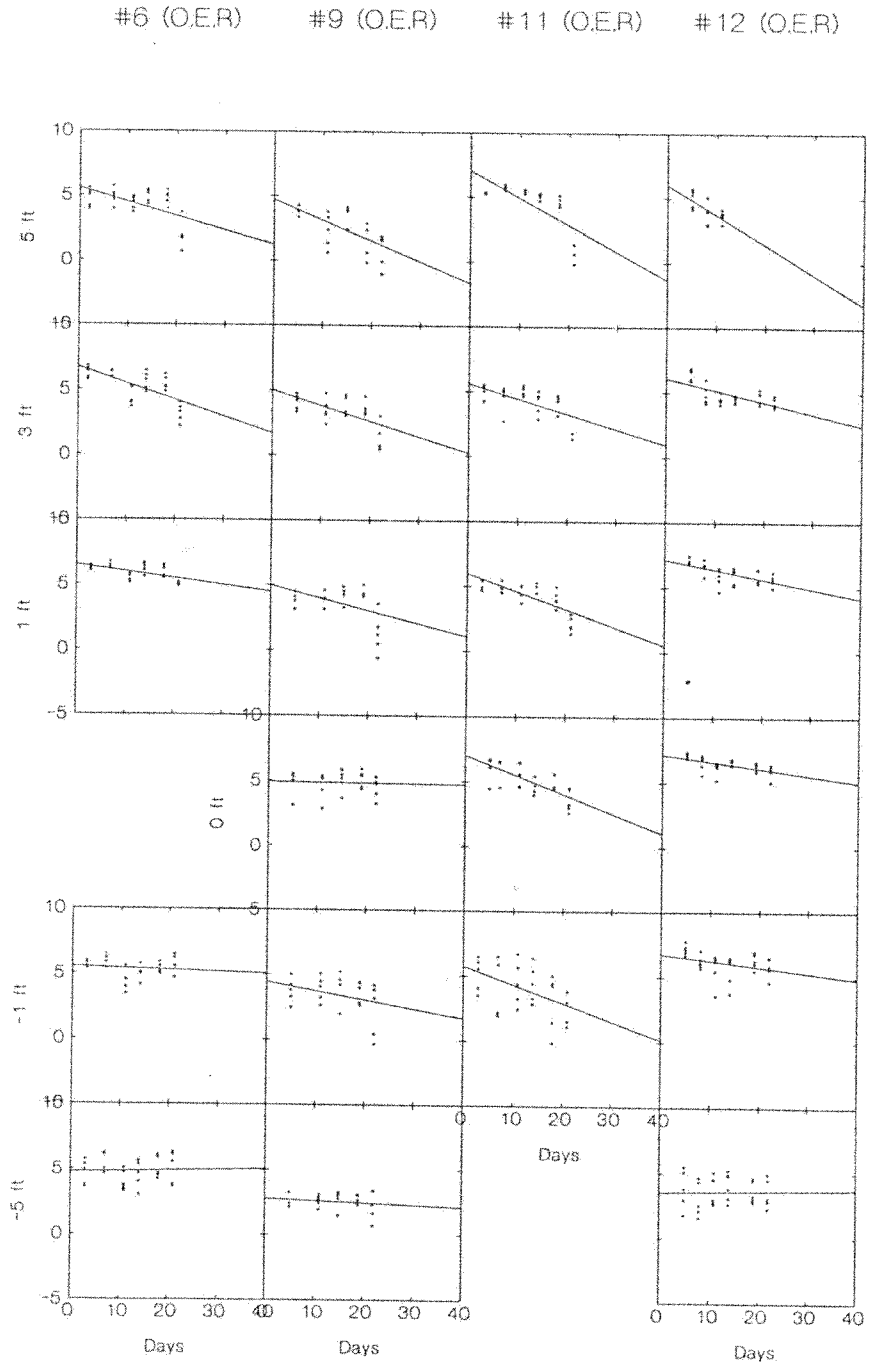


Figure 21. Regressions of ln(egg abundance) against days since spawn for 1995 transects. The line represents the best estimate of the egg loss rate (-Z) at each depth. O=oiled, R=rocky substrate, E=wave-exposed, P=wave-protected.

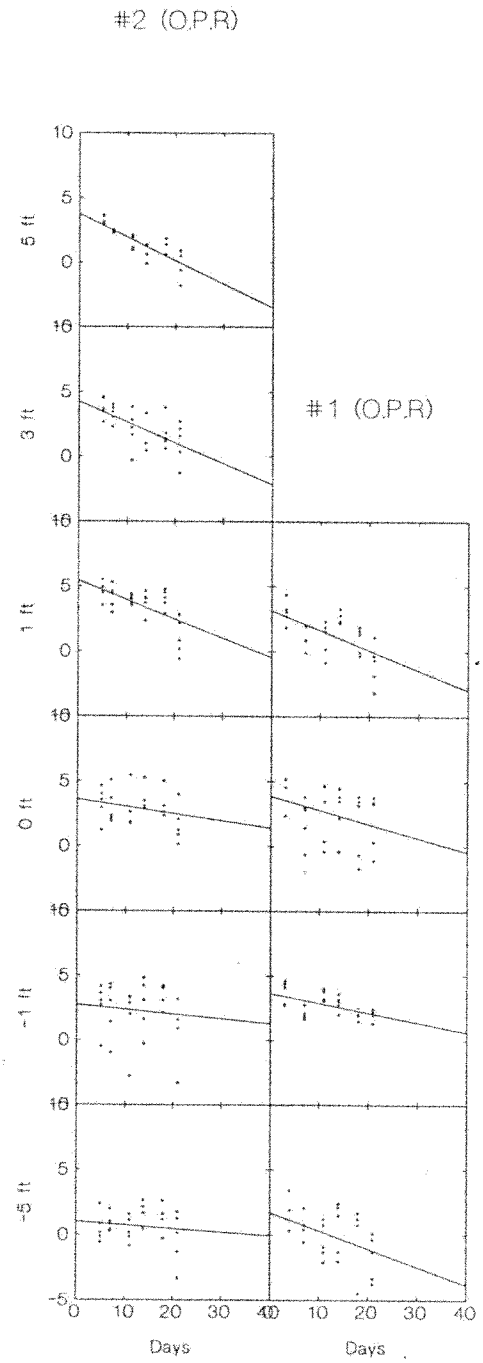


Figure 21 (continued). Regressions of ln(egg abundance) against days since spawn for 1995 transects. The line represents the best estimate of the egg loss rate (-Z) at each depth. O=oiled, R=rocky substrate, E=wave-exposed, P=wave-protected.

Table 15. Summary of 1995 egg loss regressions from each transect by depth. R=rocky substrate, P=wave-protected, E=wave-exposed.

	Transect	**1**	**2**	**6**	**9**	**11**	**12**
	Habitat classificatio	R,P	R,P	R,E	R,E	R,E	R,E
Depth (ft)							
5	slope (-Z)		-0.182	-0.108	-0.160	-0.210	-0.231
	intercept		3.766	5.569	4.726	7.059	6.023
	R^2		0.674	0.277	0.411	0.527	0.420
	p-value		0.000	0.003	0.001	0.000	0.009
3	slope (-Z)		-0.159	-0.126	-0.119	-0.115	-0.090
	intercept		4.238	6.735	5.004	5.598	6.100
	R^2		0.381	0.455	0.335	0.336	0.408
	p-value		0.000	0.000	0.002	0.001	0.000
1	slope (-Z)	-0.154	-0.147	-0.050	-0.097	-0.137	-0.074
	intercept	3.166	5.438	6.511	4.998	6.006	7.158
	R^2	0.338	0.364	0.324	0.174	0.557	0.402
	p-value	0.001	0.000	0.001	0.038	0.000	0.000
0	slope (-Z)	-0.107	-0.054		-0.004	-0.148	-0.053
	intercept	3.875	3.599		4.892	7.032	7.175
	R^2	0.105	0.055		0.001	0.519	0.321
	p-value	0.080	0.213		0.899	0.000	0.001
-1	slope (-Z)	-0.075	-0.036	-0.011	-0.069	-0.140	-0.047
	intercept	3.638	2.734	5.538	4.455	5.771	6.763
	R^2	0.259	0.010	0.009	0.093	0.213	0.089
	p-value	0.004	0.604	0.616	0.139	0.012	0.110
-5	slope (-Z)	-0.138	-0.027	0.007	-0.016		0.005
	intercept	1.669	1.011	4.780	2.768		3.522
	R^2	0.194	0.015	0.002	0.023		0.001
	p-value	0.017	0.519	0.820	0.465		0.880

There appear to be no distinct differences in 1995 egg loss rates between the two wave exposure categories (Figure 22). Similar patterns in egg loss rates with both increased depth and increased air exposure occurred at both wave-exposed and wave-protected transects.

Egg loss rates in 1995 seem to be lower where large brown kelp is the dominant vegetation (Figure 23). The majority of the data points are at quadrats and depths where large brown kelps are not dominant, so the true pattern of egg loss in these categories may not be clear from the graphical analysis.

Egg loss rates for all levels of both depth and air exposure sampled in 1995 are also shown (Figure 24). Increased depth relative to mean low water corresponds to a decrease in egg loss rate, as in previous years. This is the clearest pattern from the graphical analysis of 1995 egg loss data.

In all three covariates evaluated in 1995 the same pattern is seen. Increased bird abundance is associated with a decrease in egg loss rates in 1995 (Figure 25), and the same pattern occurs with increased glaucous winged gulls (Figure 26). Increased abundance of fish is also correlated with a slight decrease in egg loss rates (Figure 27). These results seem highly counterintuitive (the presence of known predators reducing egg loss rates), and suggest that predator abundance is related to some other variable that affects egg loss.

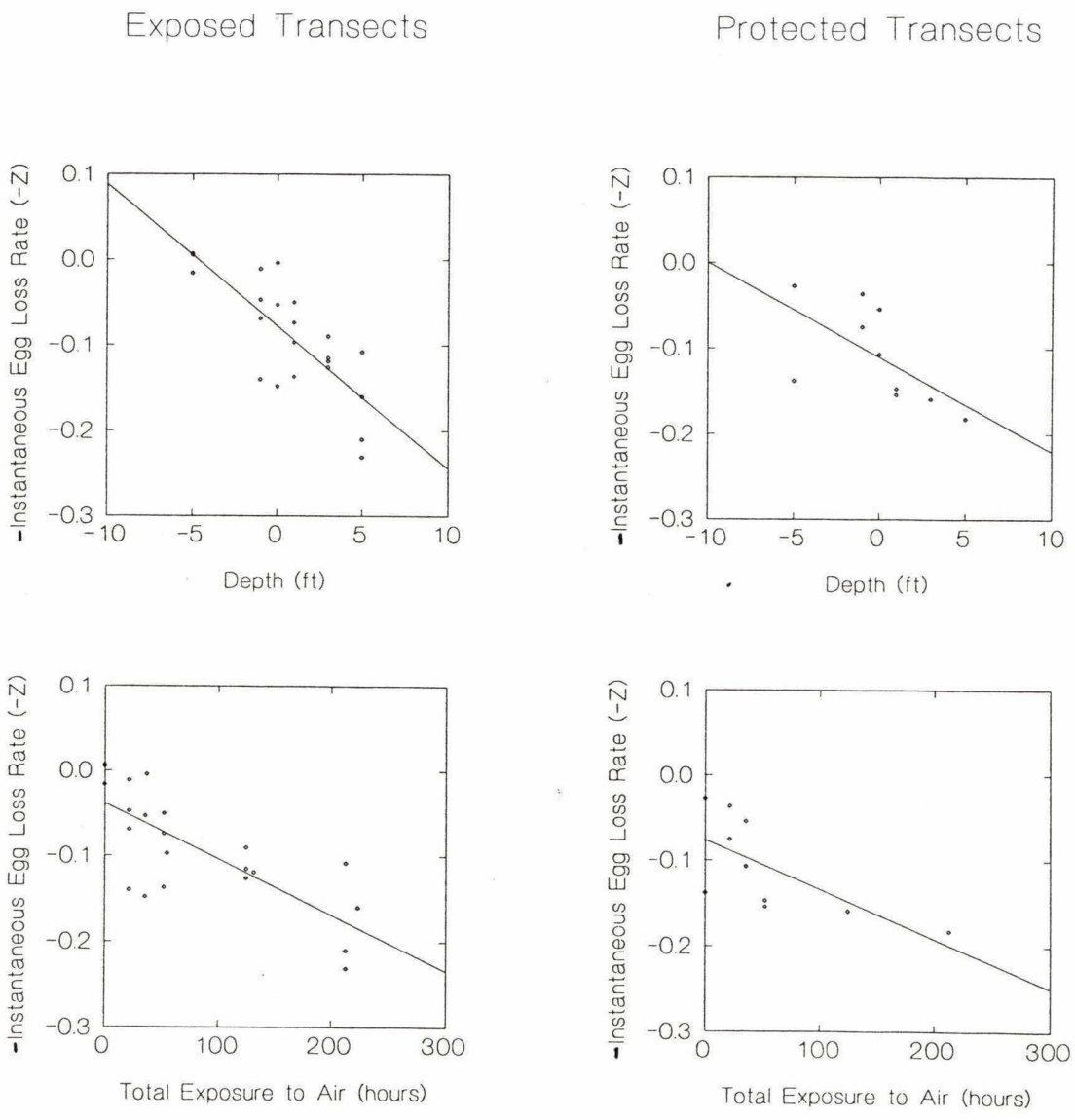


Figure 22. Egg loss rates for wave-exposed and wave-protected transects in 1995. Egg loss rates are plotted against both depth and air exposure.

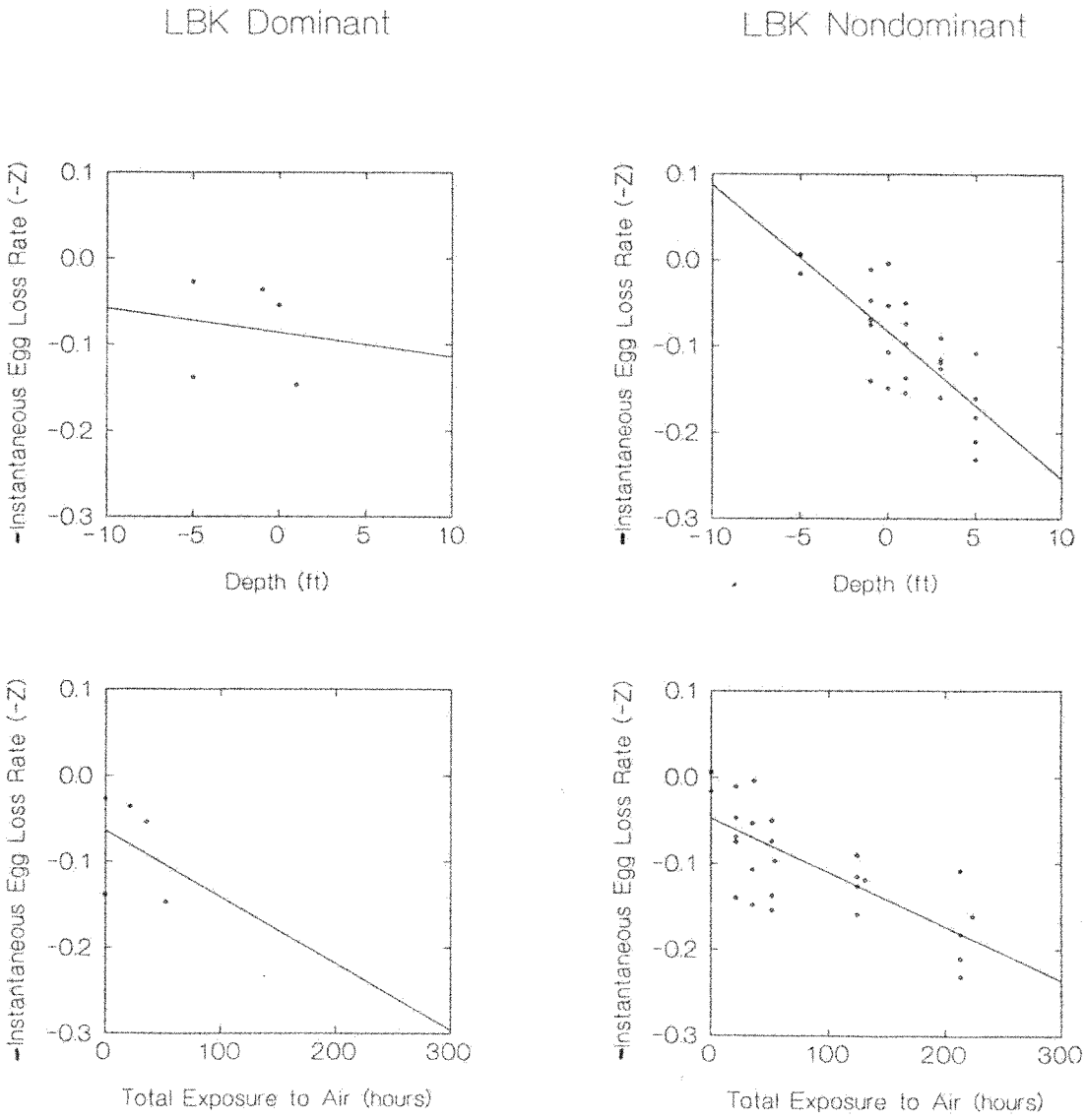


Figure 23. Egg loss rates for each kelp type category for 1995. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK), and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted in each category against both depth and air exposure.

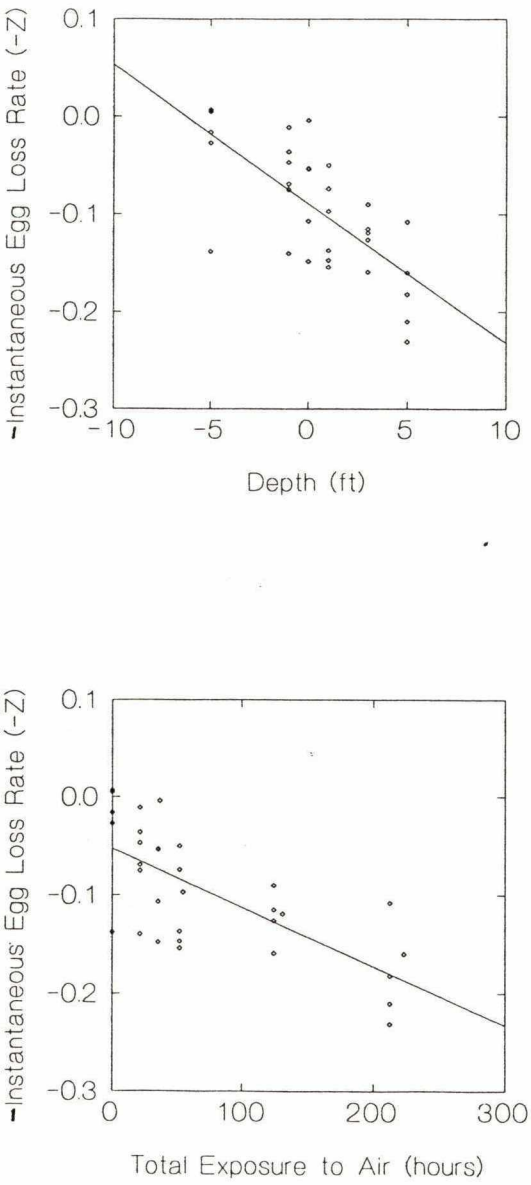


Figure 24. Egg loss rates against depth and air exposure for 1995.

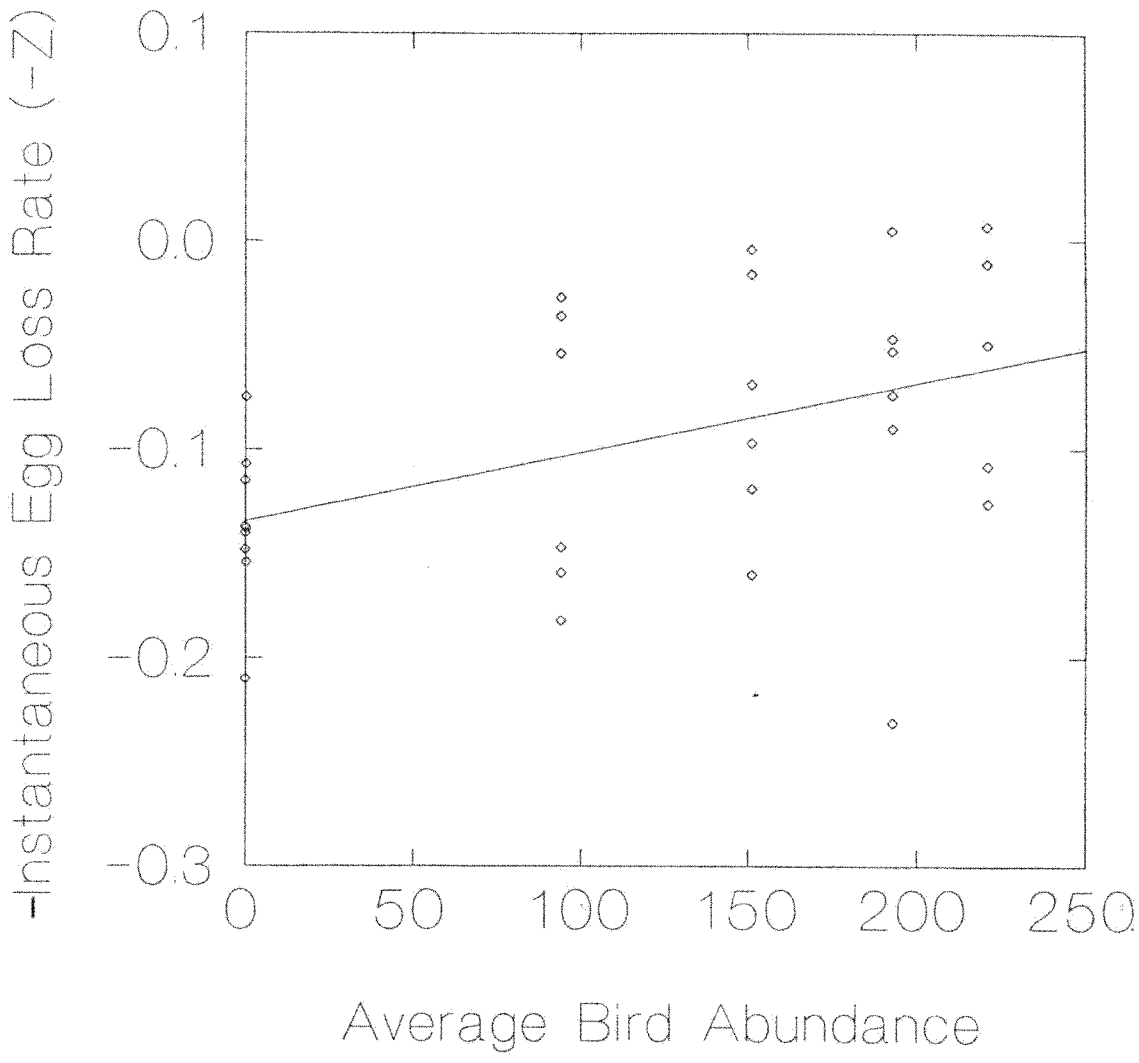


Figure 25. Egg loss rates against average bird abundance at 1995 transects.

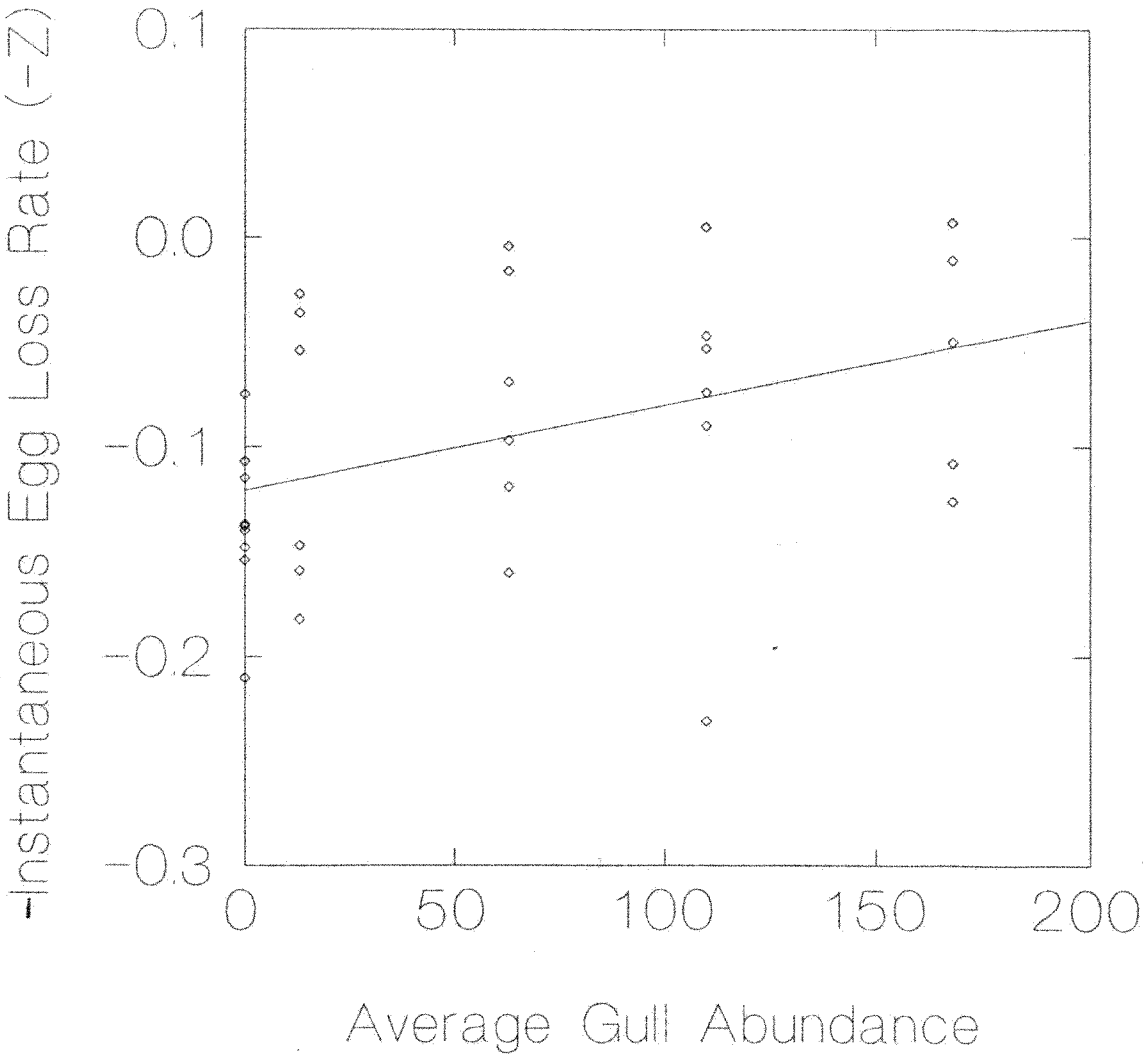


Figure 26. Egg loss rates against average glaucous winged gull abundance at 1995 transects.

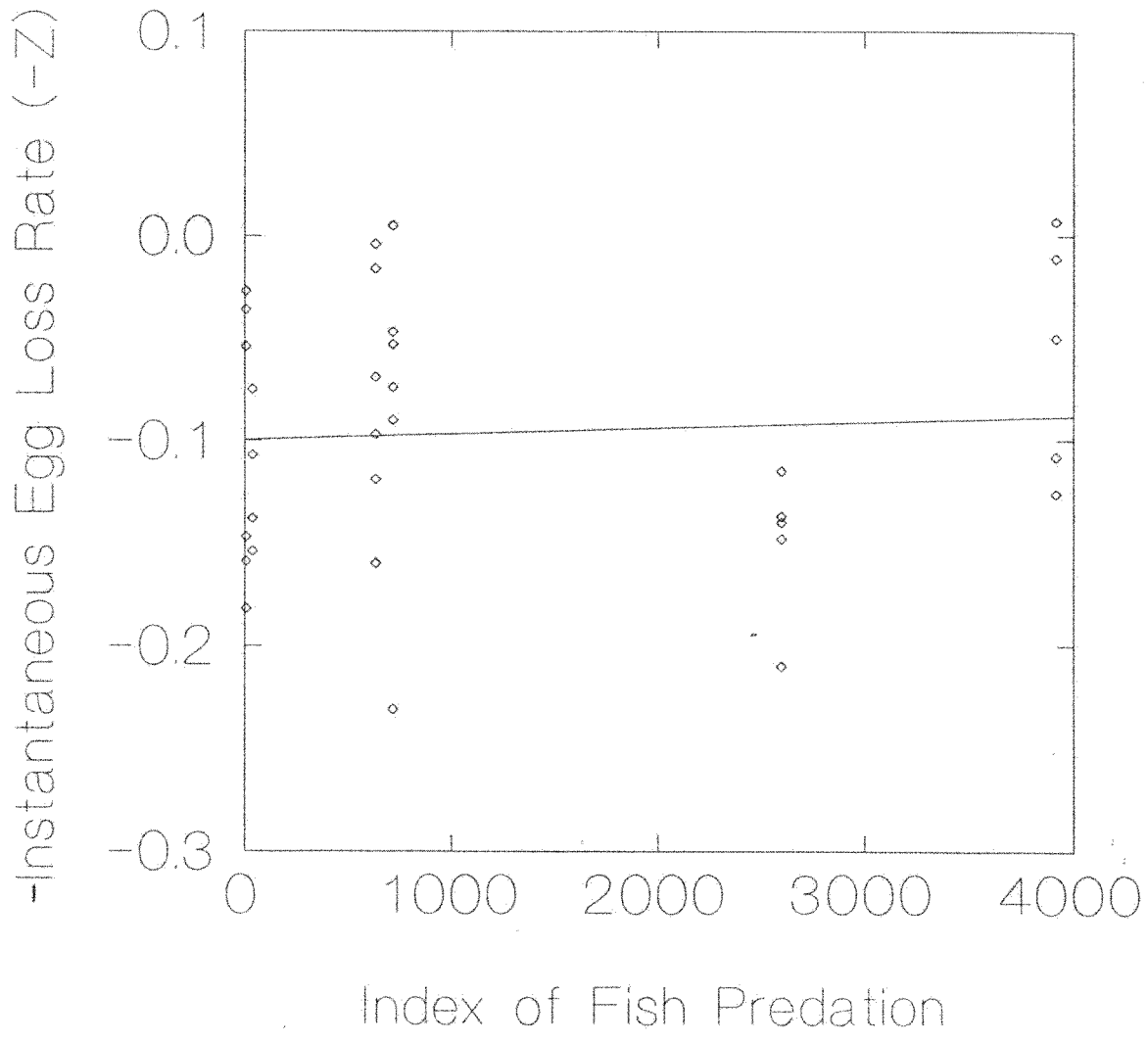


Figure 27. Egg loss rates against fish predation index at 1995 transects.

Analysis of Covariance

I performed an analysis of covariance on the 1995 egg loss data, as with previous years' data. The dependent variable was ln(egg abundance) with days since spawn as a covariate. Categorical variables available in 1995 included depth, wave exposure and kelp type. Two interaction terms between factors were available for this analysis, depth*wave exposure, and kelp type*wave exposure, as well as a number of covariate interactions. Most factors and interaction terms were significant with the exception of the kelp type variable, the wave exposure*days since spawn, and the kelp type*days since spawn interactions (Table 16). The covariate term, days since spawn, was highly significant, explaining the most variability in the data. The analysis itself explained 58% of the variability in ln(egg abundance) data for 1995.

Factorial Analyses

The habitat variables available for modeling egg loss rates in 1995 were depth, wave exposure, and kelp type. Covariates included were the average number of glaucous winged gulls and average number of total birds of all species at each transect, as well as average catch per unit effort of fish at each transect weighted by consumption. A separate analysis using air exposure in the place of depth was also performed.

The best model of egg loss rates in 1995 included just two variables, depth and average bird abundance (Table 17). This model explained 78.4% of the variation in egg loss rates. Graphical analysis of the relationship between depth and egg loss rate shows that

Table 16. Results of analysis of covariance of 1995 ln(egg abundance) data.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

n: 920 Multiple R: 0.762 Squared Multiple R: 0.580

Source	Sum of Squares	DF	MSE	F-Ratio	P
Wave exposure*Depth	33.164	5	6.633	3.575	0.003
Wave exposure*Kelp type	21.394	1	21.394	11.53	0.001
Wave exposure*Days	4.076	1	4.076	2.197	0.139
Kelp type*Days	0.520	1	0.520	0.280	0.597
Depth*Days	64.721	5	12.944	6.976	0.000
Kelp type	5.846	1	5.846	3.151	0.076
Wave exposure	62.194	1	62.194	33.520	0.000
Depth	94.803	5	18.961	10.219	0.000
Days since spawn	166.272	1	166.272	89.613	0.000
Error	1666.196	898	1.855		

Table 17. Results of factorial analysis of 1995 egg loss rates.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 32 Multiple R: 0.886 Squared Multiple R: 0.784

Source	Sum of Squares	DF	MSE	F-Ratio	P
Depth	0.073	5	0.015	13.675	0.000
Bird abundance	0.030	1	0.030	28.449	0.000
Error	0.027	25	0.001		

the rate of egg loss seems to be higher at shallower depths (Figure 24). This is a similar result to that of previous years. However, it appears that an inverse relationship exists between egg loss rates and bird abundance; egg loss rates are higher at lower bird abundance (Figure 25). This is not the expected result, and is the opposite relationship of that found in 1994. Therefore, the observed relationship between bird abundance and egg loss rates is probably a reflection of some other variable.

Exclusion of the bird covariates from the factorial analysis leads to a model explaining 53.9% of the variability in egg loss rates, and containing only the depth term (Table 18).

1.3.5. 1990 and 1991 combined analysis

I applied the same methods to analyze the combined 1990 and 1991 data as were used for the individual years. An analysis of covariance was performed on the ln(egg abundance) data using all available habitat variables. To model egg loss rates, the slope (Z) of linear regressions fitted to the ln(egg abundance) data at each depth for each transect in 1990 and 1991 was used as the dependent variable for factorial analyses.

Graphical Analyses

Combined 1990 and 1991 egg loss data were broken down by habitat variables for graphical analysis using the same techniques as for individual years. Variability associated with the substrate variable was accounted for by choosing only transects

Table 18. Results of factorial analysis of 1995 egg loss rates, excluding the average bird abundance variable.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 32 Multiple R: 0.734 Squared Multiple R: 0.539

Source	Sum of Squares	DF	MSE	F-Ratio	P
Depth	0.067	5	0.013	6.075	0.001
Error	0.057	26	0.002		

occurring within the rocky and boulder substrates (except where the substrate variable itself is examined).

Egg loss rates (Z) plotted against air exposure and depth in each of the wave exposure categories shows that egg loss is higher in wave-protected areas than in wave-exposed areas (Figure 28). It also appears that egg loss rates are higher at shallower depths. The exposed category is represented by three transects, the protected category by eight.

Graphical analysis of egg loss in oiled/unoiled breakdown shows a distinct difference in egg loss between the two categories (Figure 29). Egg loss rates appear to be higher in previously oiled areas than in unoiled areas. The unoiled category includes data from six transects, the oiled data from five, and as in the previous figures egg loss rate appears to decrease with depth.

Egg loss rates for the combined years 1990 and 1991 plotted by substrate type show that there are few data points from substrates other than rocky (Figure 30). The rocky substrate occurred at eleven transects, the boulder at one transect, and the gravel at three transects. Within the rocky substrate, egg loss rates decrease as depth increases, while data from the gravel substrate show the opposite effect. This may be a result of the small number of transects within the gravel type substrate.

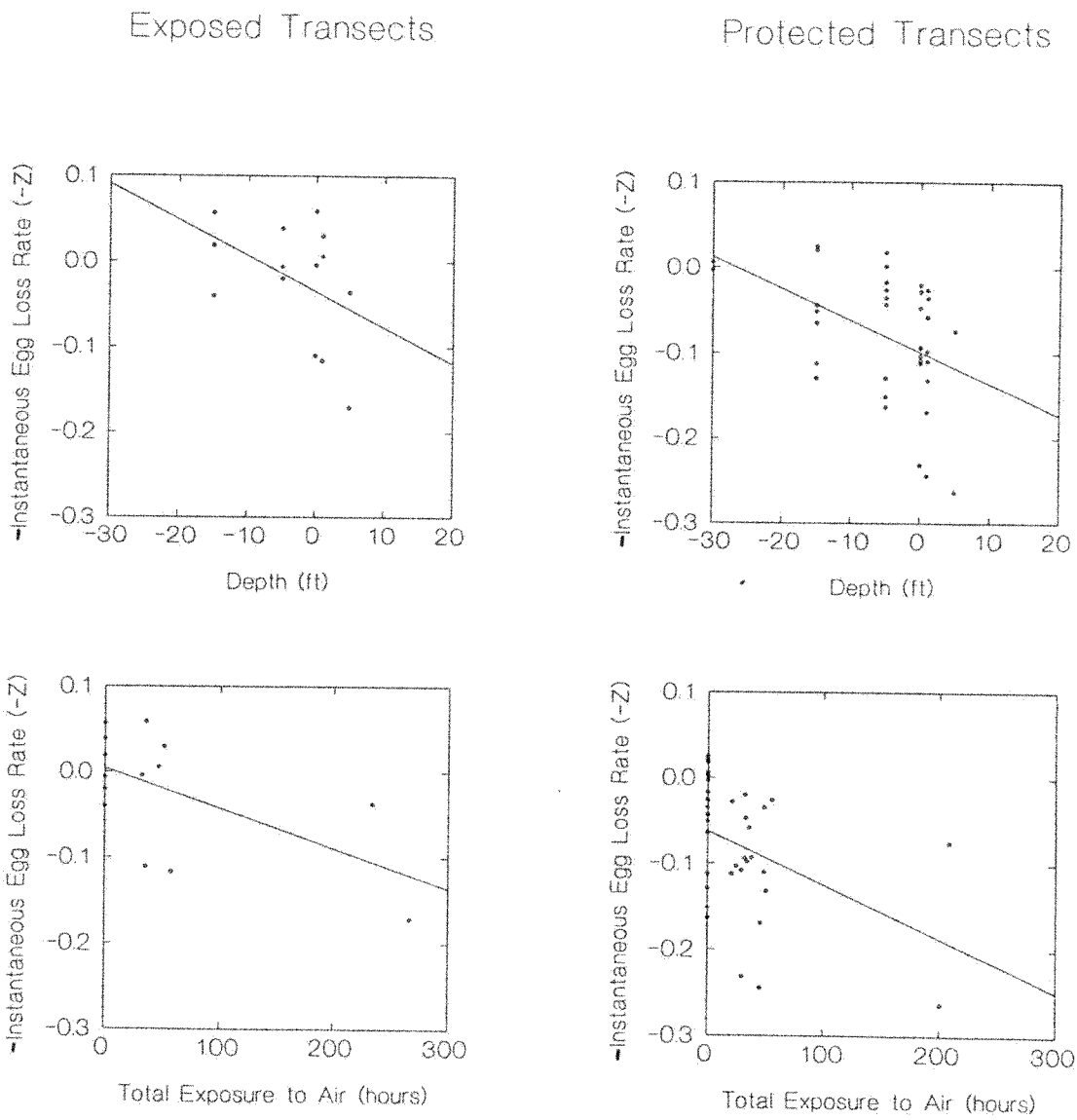


Figure 28. Egg loss rates for wave-exposed and wave-protected transects for 1990-1991 combined. Data taken from rocky and boulder substrates only.

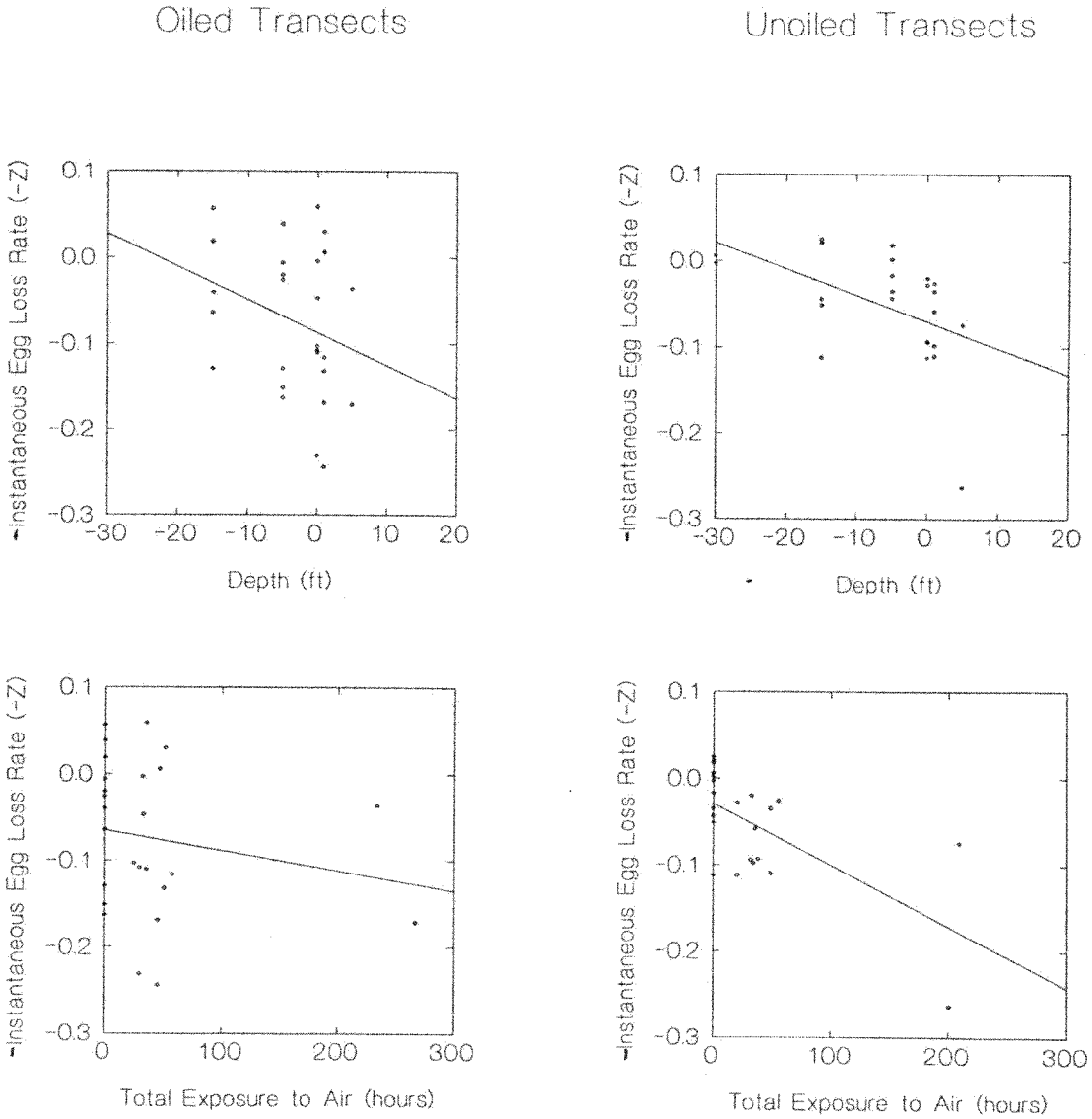


Figure 29. Egg loss rates at previously oiled and unoiled transects for 1990-1991 combined. Data taken from rocky and boulder substrates only.

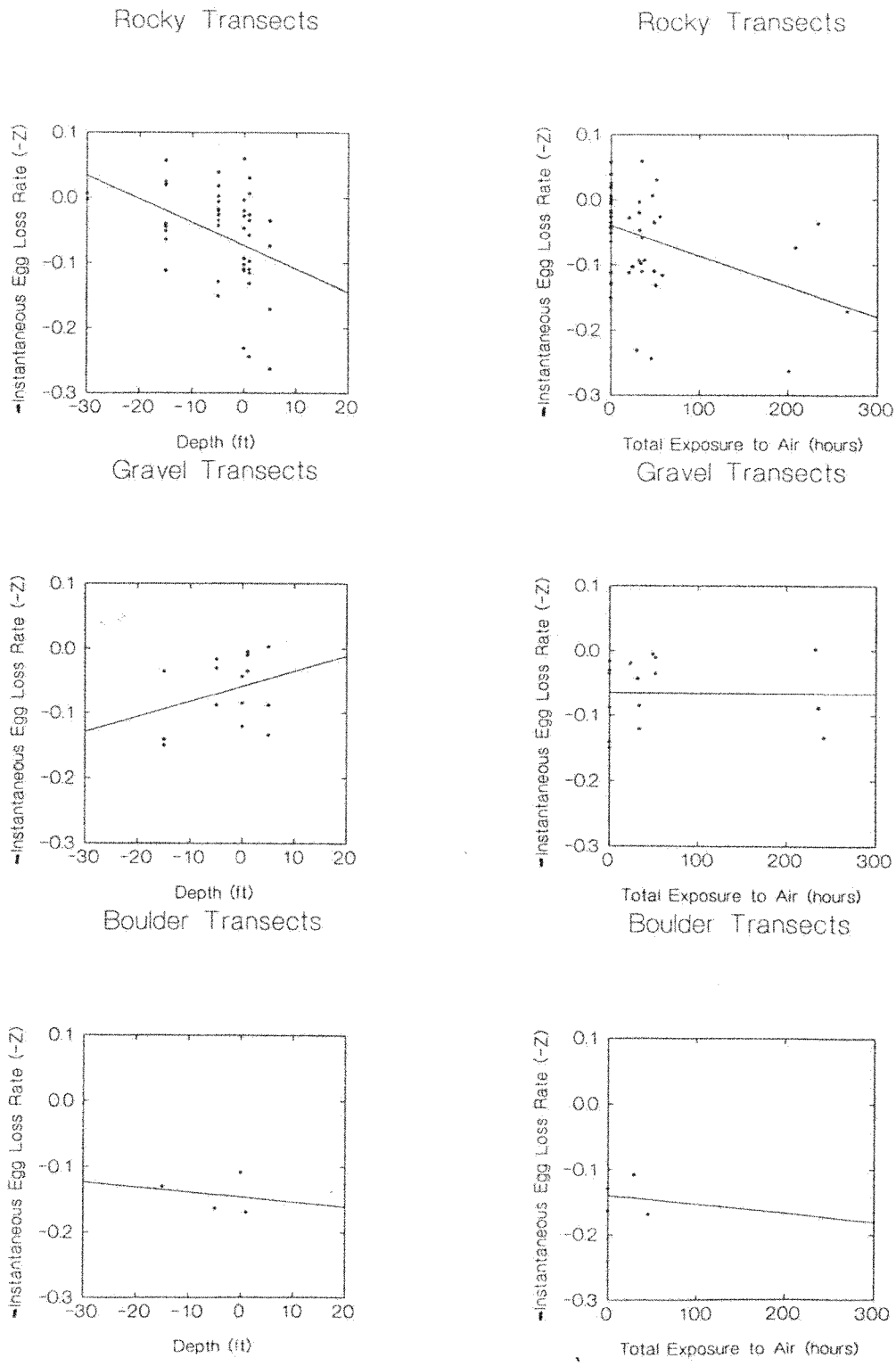


Figure 30. Egg loss rates in each substrate type sampled in 1990-1991 combined.

A plot of egg loss rates from each year against both depth and air exposure shows egg loss may have been higher in 1990 than in 1991 (Figure 31). This suggests that interannual variability may be important when considering egg loss rates.

A problem arises when comparing egg loss rates in the two kelp type categories. Large brown kelp seems to be more likely to dominate at subtidal depths, so there are few data points for this classification above mean low water (Figure 32). This makes it hard to distinguish the patterns in egg loss resulting from this variable, since it is difficult to determine which effects are due to depth and which to kelp type.

The final habitat variable, depth, shows the familiar pattern of increasing egg loss at higher depths (Figure 33). The effect of depth on egg loss rates seems to be the most consistent from this and previous analyses.

Analysis of Covariance

I performed an analysis of covariance on the combined 1990-1991 ln(egg abundance) data with days since spawn as the covariate. This analysis also included all the habitat variables available for both years as well as a number of interaction terms. The results of the ANCOVA explained 42.1% of the variation in ln(egg abundance) data, with the wave exposure term accounting for the most variability of all the terms included in the model (Table 19). The majority of interaction terms in the model were significant, as well as all main effects except depth.

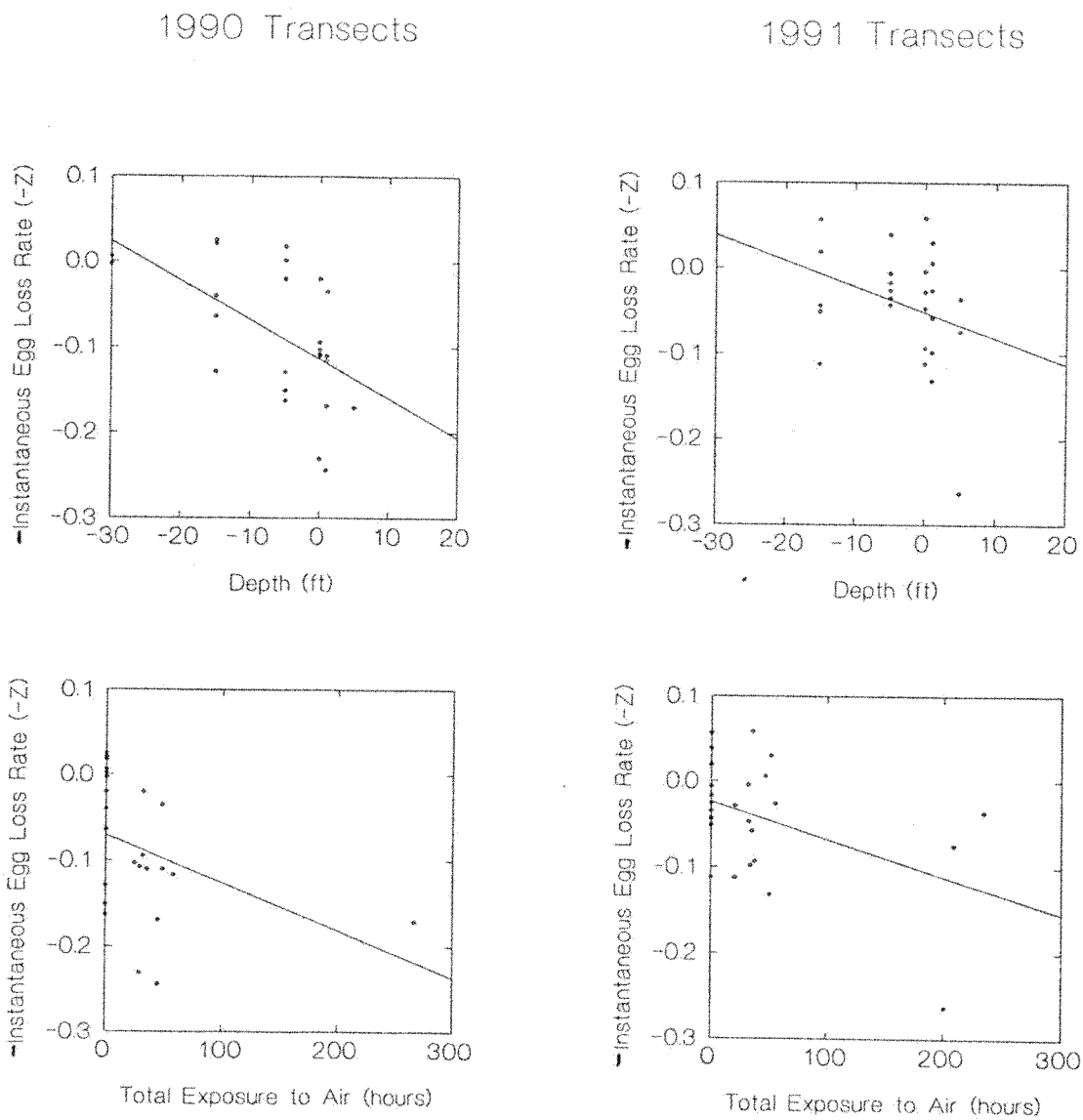


Figure 31. Egg loss rates from each year, 1990 and 1991. Egg loss rates are plotted against both depth and air exposure. Data are from rocky and boulder substrates only.

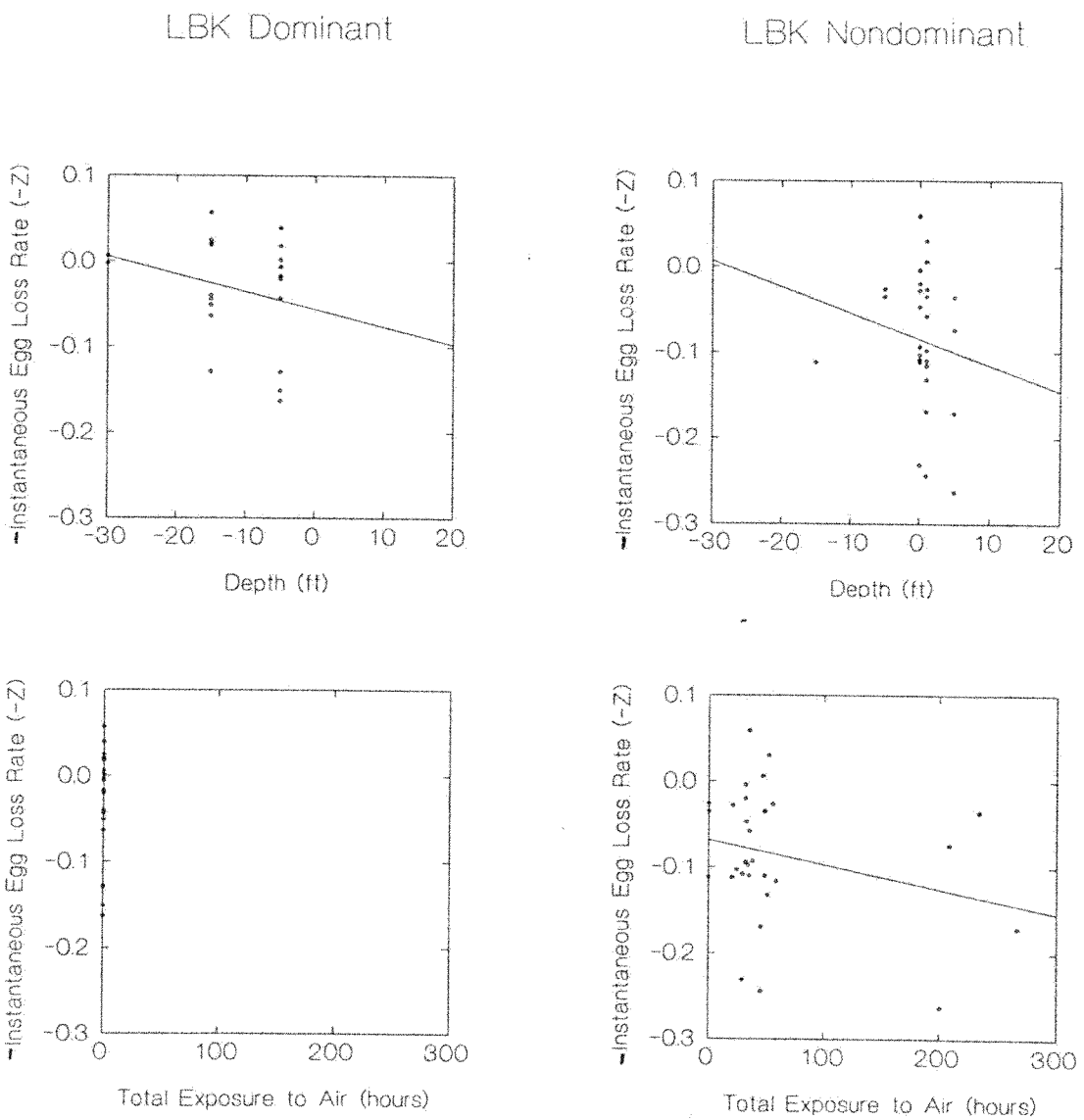


Figure 32. Egg loss rates in each kelp type category for 1990-1991 combined. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK), and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted against both depth and air exposure, data are from rocky and boulder substrates only.

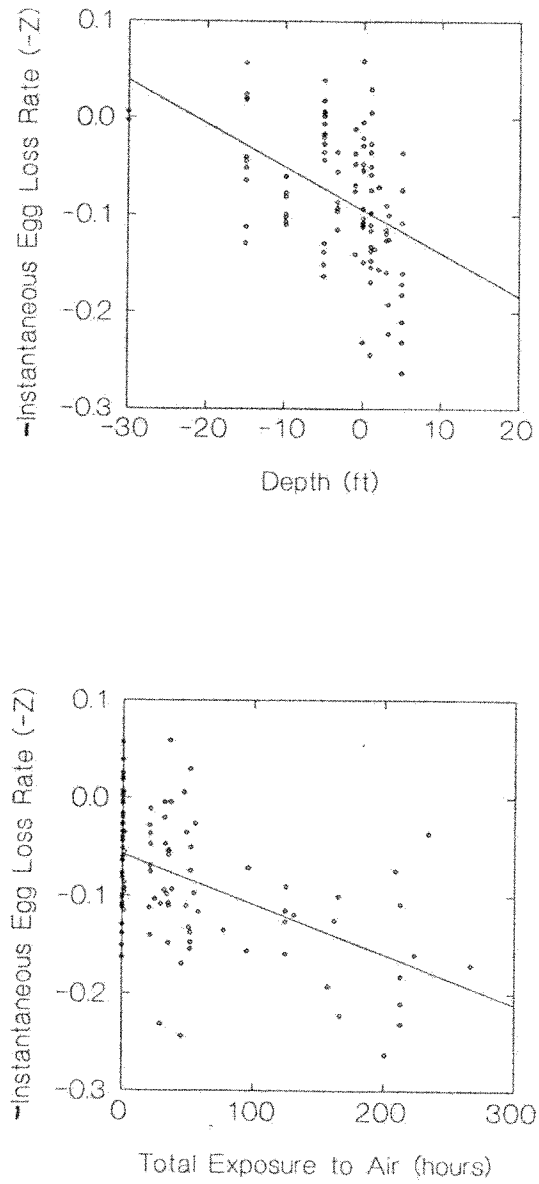


Figure 33. Egg loss rates against depth and air exposure for 1990 and 1991 combined. Data are from rocky and boulder substrates only.

Table 19. Results of analysis of covariance of the combined 1990 and 1991 ln(egg abundance) data.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

N: 2969 Multiple R: 0.649 Squared Multiple R: 0.421

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Oiled/unoiled*Year	8.484	1	8.484	4.041	0.045
Kelp type*Oiled/unoiled*Days	0.103	1	0.103	0.049	0.825
Kelp type*Wave exposure*Days	0.312	1	0.312	0.148	0.700
Kelp type*Year*Days	14.814	1	14.814	7.055	0.008
Kelp type*Substrate type*Days	13.627	2	6.813	3.245	0.039
Oiled/Unoiled*Year*Days	127.827	1	127.827	60.878	0.000
Wave exposure*Year*Days	8.355	1	8.355	3.979	0.046
Kelp type*Oiled/unoiled	61.854	1	61.854	29.458	0.000
Kelp type*Wave exposure	32.968	1	32.968	15.701	0.000
Kelp type*Year	1.784	1	1.784	0.849	0.357
Kelp type*Substrate type	11.417	2	5.709	2.719	0.066
Oiled/Unoiled*Year	74.966	1	74.966	35.703	0.000
Wave exposure*Year	5.868	1	5.868	2.794	0.095
Depth*Days	31.184	5	6.237	2.970	0.011
Year	126.239	1	126.239	60.122	0.000
Oiled/Unoiled	773.648	1	773.648	368.454	0.000
Substrate type	404.301	2	202.151	96.275	0.000
Kelp type	14.270	1	14.270	6.796	0.009
Wave exposure	1121.976	1	1121.976	534.347	0.000
Depth	12.447	5	2.489	1.186	0.314
Days since spawn	130.874	1	130.874	62.329	0.000
Error	6164.765	2936	2.100		

Factorial Analyses

I carried out a number of factorial analyses on the combined 1990 and 1991 data using instantaneous egg loss rate (Z) as the dependent variable. These analyses attempted to measure the effects of the various habitat variables seen in the graphical analyses and any interaction effects between the variables. The habitat variables: year, substrate, oiled/unoiled, wave exposure, and depth were available for both years as independent variables.

Due to the unbalanced nature of the sample design, a number of different subsets of the combined 1990-1991 data were modeled in order to maximize the interaction terms available. The major division of data was in the substrate variable. Subsets of data from the rocky substrate only, data from rocky and boulder substrates, and data pooled over all substrates were each analyzed. To maximize the number of interaction terms, the -30 foot depth and the +5 foot depth were eliminated individually as well as simultaneously from some analyses. Appendix B of Rooper et al. (1996) includes results of all data sets modeled for the combined 1990-1991 data

The data set resulting in the best model was from all depths pooled over rocky and boulder substrates. When data were pooled over these substrates, a variety of two-way interactions could be analyzed for the remaining factors, and after sequential removal of insignificant terms a model containing the interaction terms oiled/unoiled*year, kelp type*year and kelp type*substrate type, and the habitat variables wave exposure,

oiled/unoiled, year and depth results (Table 20). This model explains about 77.7% of the variability in egg loss rates for the combined years 1990 and 1991.

The presence of the substrate type*kelp type variable probably reflects the small number of transects in each substrate, as well as the confounding problem of kelp type and depth. Removal of this term leads to a model containing only the year*oiled/unoiled interaction term, and the habitat variables year, oiled/unoiled, wave exposure and depth (Table 21). This model explains 73.4% of the variability in egg loss rates for 1990 and 1991.

Depth and the interaction term accounted for the most variability in egg loss rates, suggesting that these two were the most important factors affecting egg loss in 1990 and 1991. The significance of the interaction term implies that the condition oiled/unoiled (location) had different effects on egg loss in the individual years. From the individual analyses performed on each year's data, it is evident that oiled/unoiled condition was very important in determining egg loss in 1990, but insignificant in determining egg loss in 1991.

Average negative egg loss rates (-Z) and corresponding standard errors are summarized for each significant habitat factor (Table 22). These were calculated from Tables 2 and 6 for all levels of the depth, wave exposure, year and oiled/unoiled categories. The average egg loss rate decreased at deeper depths, and the average egg loss rate is higher for oiled transects than unoiled transects when both

Table 20. Results of factorial analysis of combined 1990 and 1991 egg loss rates. Data from rocky and boulder substrates only, with all depths.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 51 Multiple R: 0.882 Squared Multiple R: 0.777

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Substrate type	0.008	1	0.008	5.037	0.031
Kelp type*Year	0.008	1	0.008	4.775	0.035
Year*Oiled/Unoiled	0.043	1	0.043	26.391	0.000
Year	0.008	1	0.008	4.786	0.035
Oiled/Unoiled	0.026	1	0.026	15.841	0.000
Wave exposure	0.036	1	0.036	21.796	0.000
Depth	0.024	5	0.005	2.922	0.025
Error	0.064	39	0.002		

Table 21. Results of factorial analysis of combined 1990 and 1991 egg loss rates, with the kelp type*substrate type interaction removed.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 51 Multiple R: 0.857 Squared Multiple R: 0.734

Source	Sum of Squares	DF	MSE	F-Ratio	P
Year*Oiled/unoiled	0.046	1	0.046	24.649	0.000
Oiled/unoiled	0.025	1	0.025	13.627	0.001
Wave exposure	0.036	1	0.036	19.090	0.000
Year	0.009	1	0.009	4.828	0.034
Depth	0.054	5	0.011	5.753	0.000
Error	0.077	41	0.002		

Table 22. Average egg loss rates for 1990 and 1991 combined data for each significant habitat variable from factorial analysis. Estimates for rocky and boulder substrates only.

		1990	1991	Combined Years, Rocky and Boulder Substrates Only
Wave exposed	-Z			**-0.021**
	SE			0.018
	n			14
Wave protected	Z			**-0.079**
	SE			0.012
	n			37
Oiled	-Z	**-0.130**	**-0.003**	**-0.074**
	SE	0.016	0.015	0.017
	n	15	12	27
Unoiled	-Z	**-0.019**	**-0.075**	**-0.052**
	SE	0.015	0.017	0.013
	n	10	14	24
1990	-Z			**-0.086**
	SE			0.016
	n			25
1991	-Z			**-0.042**
	SE			0.013
	n			26

Table 22 (continued). Average egg loss rates for 1990 and 1991 combined data for each significant habitat variable from factorial analysis. Estimates for rocky and boulder substrates only.

			Combined Years, Rocky and Boulder Substrates Only
Depth	5 ft	-Z	**-0.136**
		SE	0.051
		n	4
	1 ft	-Z	**-0.087**
		SE	0.024
		n	11
	0 ft	-Z	**-0.074**
		SE	0.021
		n	12
	-5 ft	-Z	**-0.044**
		SE	0.019
		n	12
	-15 ft	-Z	**-0.032**
		SE	0.019
		n	10
	-30 ft	-Z	**0.002**
		SE	0.005
		n	2

years are combined. However, the year*oiled/unoiled interaction term shows that average egg loss rates were higher in oiled areas only in 1990, in 1991 egg loss rates were higher in unoiled areas. Egg loss was higher in 1990 than in 1991, with average egg loss rates of 0.086 (SE=0.016) and 0.042 (SE=0.013) respectively. The average egg loss rate is also higher for protected transects than for exposed transects, a counterintuitive result since transects that were exposed to higher wave forces would be expected to experience higher egg loss.

1.3.6. 1994 and 1995 combined analyses

The combination of 1994 and 1995 data includes data from transects on Montague Island only. To maximize the number of data points available, and to reduce variability associated with the substrate variable, I used data from rocky and boulder transects combined, and rocky transects only exclusively for the 1994 and 1995 analysis.

Graphical Analyses

Graphical analyses were performed on the rocky and boulder data from the combined years 1994 and 1995, in order to identify important habitat variables. Egg loss rates seem to be slightly higher in wave-protected areas than in wave-exposed areas (Figure 34). Egg loss rates plotted against air exposure and depth both show egg loss was higher in 1994 than in 1995 (Figure 35).

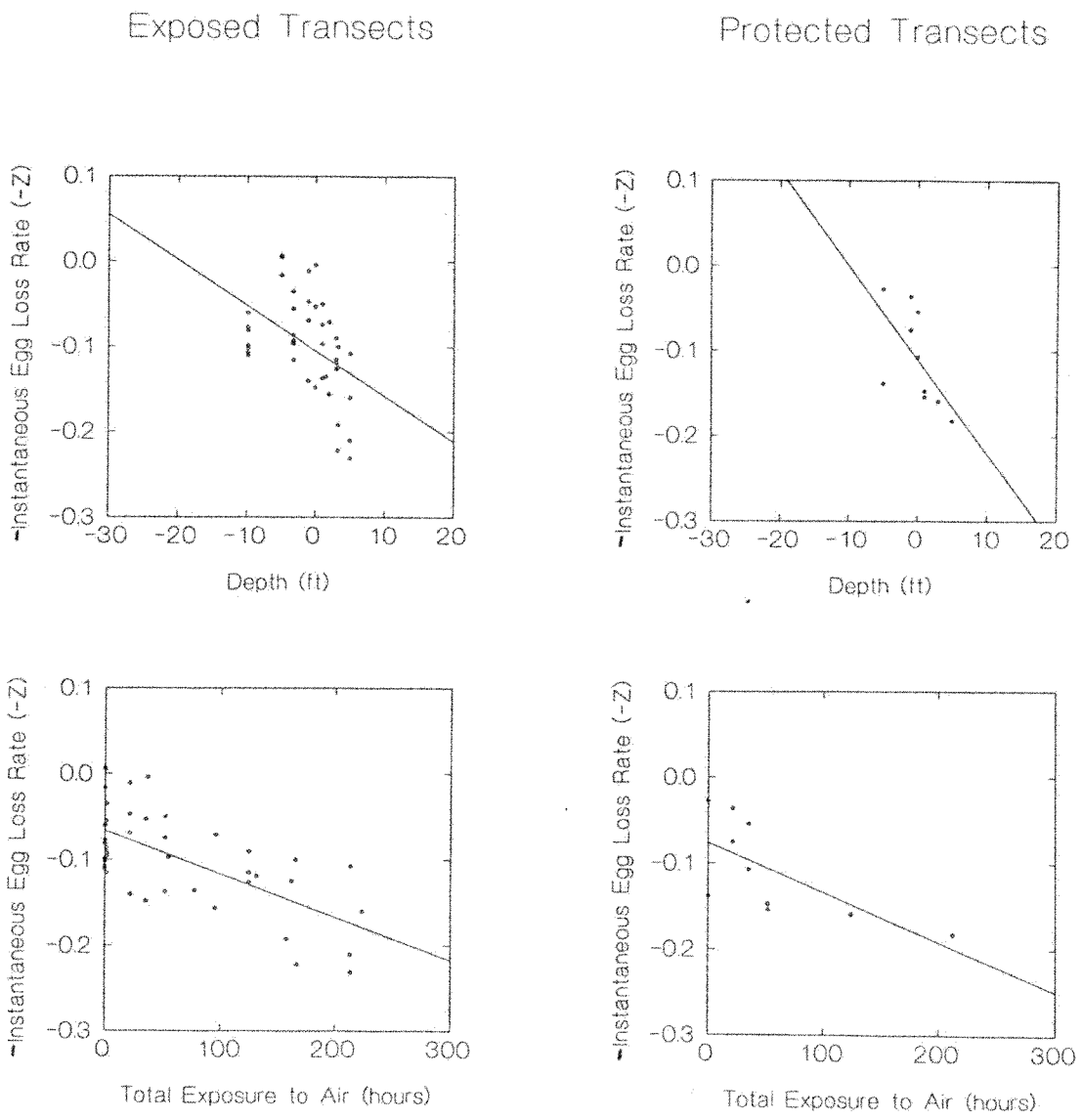


Figure 34. Egg loss rates for wave-exposed and wave-protected transects for 1994-1995 combined. Data taken from rocky and boulder substrates only, and are plotted against both depth and air exposure.

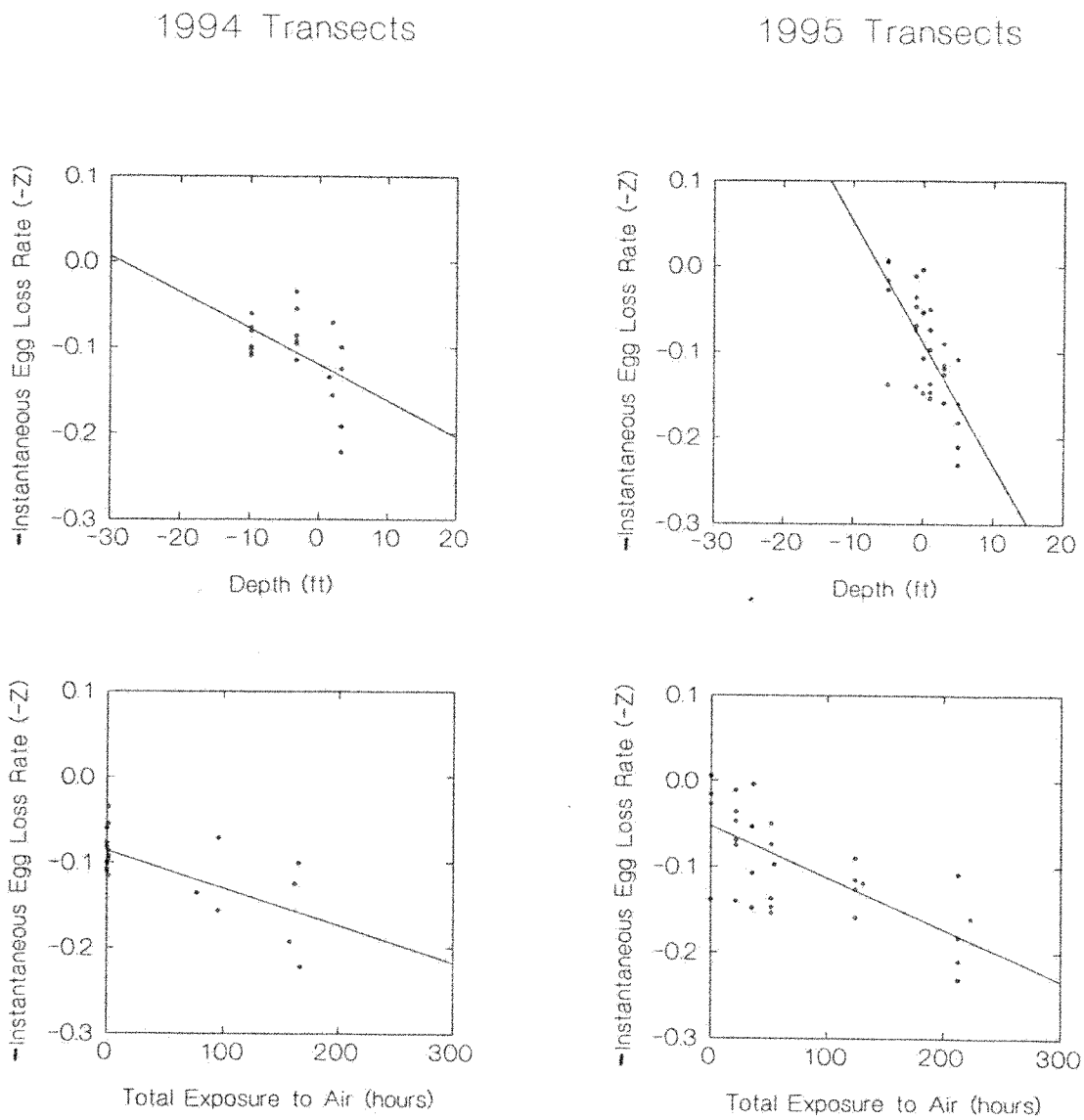


Figure 35. Egg loss rates for each year, 1994 and 1995. Egg loss rates are plotted against both depth and air exposure. Data taken from rocky and boulder substrates only.

The breakdown of egg loss rates into the two kelp type categories yields two very different pictures (Figure 36). Egg loss seems to be lower at quadrats dominated by large brown kelp when the data is plotted against depth. When egg loss rates are plotted against air exposure, the opposite trend results, egg loss is greater at stations dominated by large brown kelp. The difference may be a function of the small sample size associated with the large brown kelp dominated category, as well as the fact that large brown kelp dominates only at subtidal depths.

Depth has been an extremely important variable in the previous analysis, and that pattern continues in the combined 1994 and 1995 data set. Egg loss rates increase at higher depths, and with increasing times of air exposure over incubation (Figure 37).

Analysis of Covariance

An analysis of covariance was performed on the combined ln(egg abundance) data from 1994 and 1995 as for the previous data sets. The covariate term was days since spawn, and all available habitat variables and interaction terms were included. Days since spawn explained the most variability in ln(egg abundance) data from these two years, with the total model explaining 53.8% of the variability (Table 23). All other terms except the depth*days interaction, kelp type, wave exposure and depth were insignificant in the model.

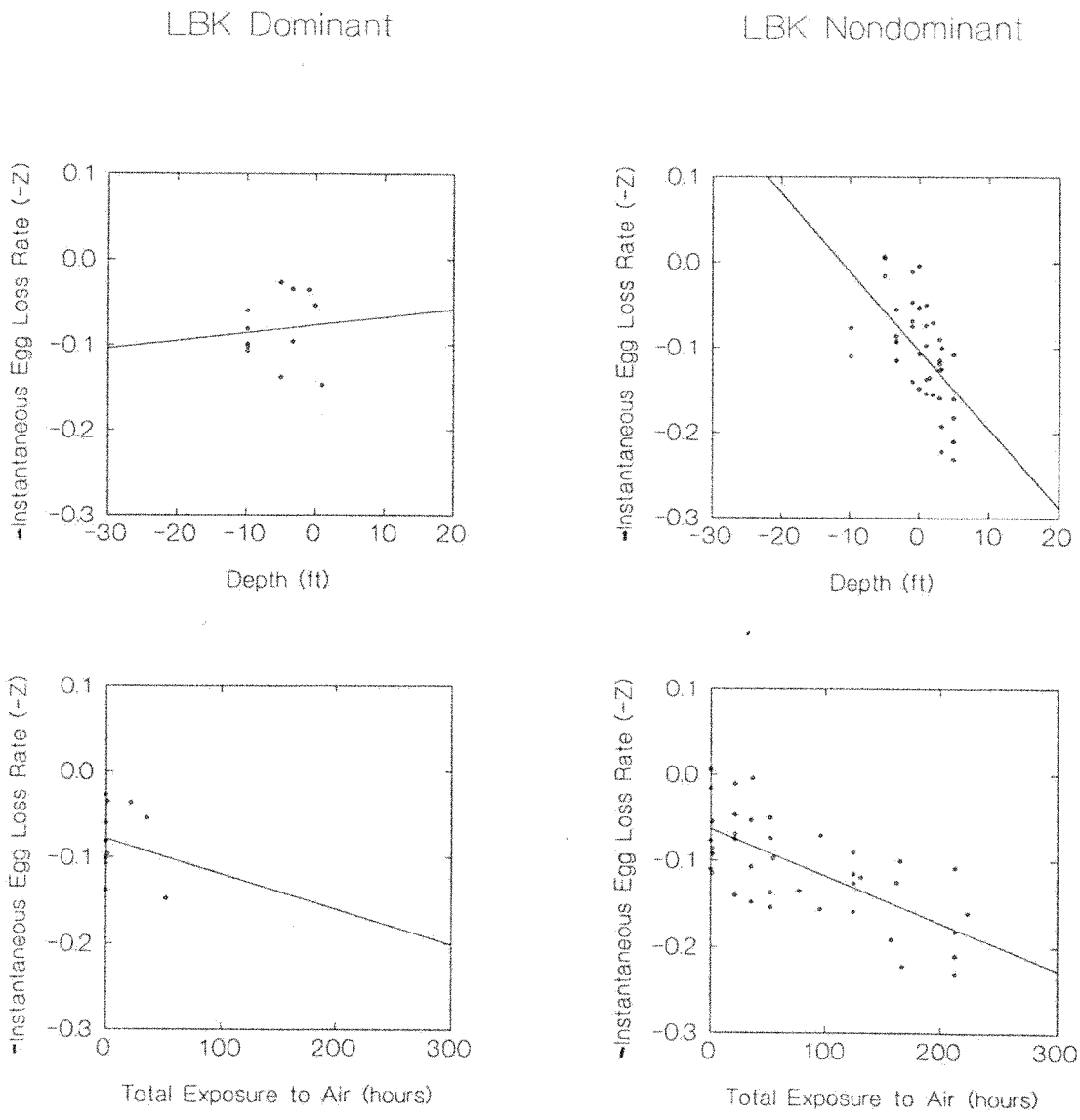


Figure 36. Egg loss rates in each kelp type category for 1994 and 1995 combined. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK) species, and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted against both depth and air exposure, and are taken from rocky and boulder transects only.

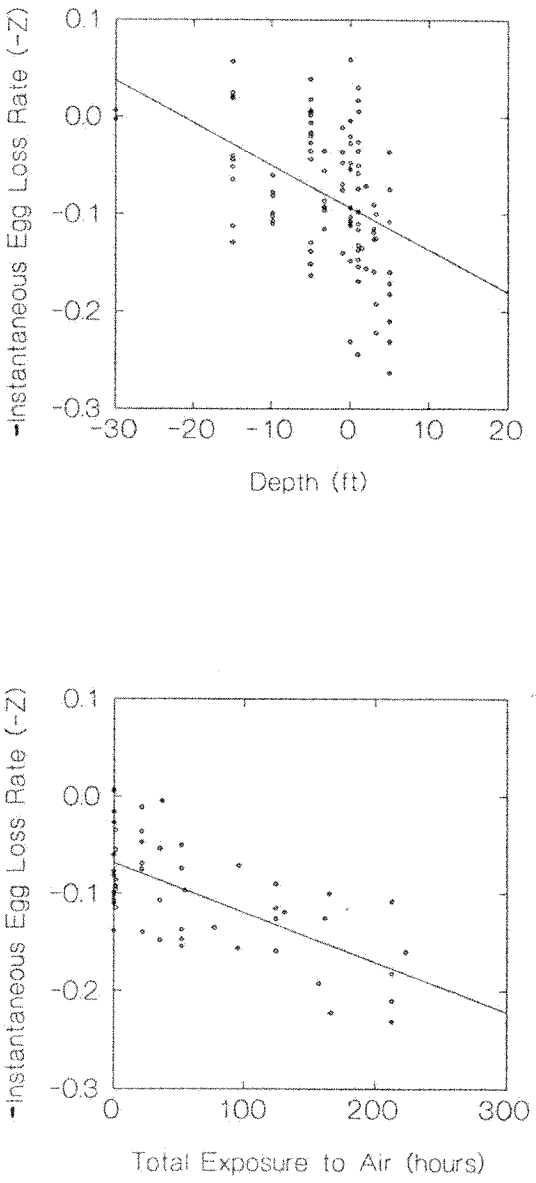


Figure 37. Egg loss rates against depth and air exposure for 1994 and 1995 combined. Data taken from rocky and boulder substrates only.

Table 23. Results of analysis of covariance of the combined 1994 and 1995 ln(egg abundance) data. Data from rocky and boulder substrates only.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

n: 1619 Multiple R: 0.734 Squared Multiple R: 0.538

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Wave exposure*Days	0.000	1	0.000	0.000	0.995
Kelp type*Year*Days	0.078	1	0.078	0.044	0.834
Kelp type*Substrate type*Days	0.038	1	0.038	0.022	0.883
Year*Days	1.769	1	1.769	1.000	0.318
Substrate type*Days	0.898	1	0.898	0.508	0.476
Kelp type*Days	0.002	1	0.002	0.001	0.975
Wave exposure*Days	2.205	1	2.205	1.247	0.264
Depth*Days	78.468	8	9.809	5.544	0.000
Kelp type*Wave exposure	1.047	1	1.047	0.592	0.442
Kelp type*Year	0.087	1	0.087	0.049	0.824
Kelp type*Substrate type	3.799	1	3.799	2.147	0.143
Year	0.038	1	0.038	0.021	0.884
Substrate type	2.202	1	2.202	1.143	0.285
Kelp type	8.127	1	8.127	4.594	0.032
Wave exposure	36.318	1	36.318	20.529	0.000
Depth	110.655	8	13.832	7.818	0.000
Days since spawn	277.492	1	277.492	156.850	0.000
Error	2807.644	1587	1.769		

Factorial Analyses

When I subjected egg loss rates from the combined years, 1994 and 1995, to a factorial analysis, a model explaining 52.4% of the variability in egg loss rates resulted (Table 24). This model is of rocky data only, and includes only the depth term. The model is consistent with the previous analyses of egg loss rates, with lower egg loss rates at deeper depths.

The second best model of egg loss rates for the combined years 1994 and 1995 came from rocky and boulder substrates combined. This subset of data represents the majority of transects in the two years, 13 of 16. Factorial analysis of habitat variables led to a model explaining 51.3% of the variability in egg loss rates (Table 25). In this model, depth is represented by air exposure. The air exposure term proves to be the most significant, explaining most of the variability by itself. The other significant terms in the model are year ($p=0.008$) and wave exposure which is marginally significant ($p=0.048$).

Average egg loss rates for significant habitat variables in both models were calculated for the combined 1994 and 1995 rocky and boulder data (Table 26). Egg loss rates were higher at wave-protected transects ($-Z=-0.108$, $SE=0.018$) than at wave-exposed transects ($-Z=-0.098$, $SE=0.009$). In 1995 egg loss rates were lower ($-Z=-0.096$, $SE=0.011$) than in 1994 ($-Z=-0.105$, $SE=0.010$). Average egg loss rates associated with each depth sampled are also summarized for rocky data only, and the results show that egg loss rates are higher at shallower depths (Table 27).

Table 24. Results of factorial analysis of combined 1994 and 1995 egg loss rates, from the rocky substrate only.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 41 Multiple R: 0.724 Squared Multiple R: 0.524

Source	Sum of Squares	DF	MSE	F-Ratio	P
Depth	0.076	8	0.010	4.400	0.001
Error	0.069	32	0.002		

Table 25. Results of factorial analysis of combined 1994 and 1995 egg loss rates from rocky and boulder substrates. For this analysis depth was replaced by time of air exposure.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 53 Multiple R: 0.716 Squared Multiple R: 0.513

Source	Sum of Squares	DF	MSE	F-Ratio	P
Air exposure	0.080	1	0.080	49.659	0.000
Year	0.013	1	0.013	7.719	0.008
Wave exposure	0.007	1	0.007	4.122	0.048
Error	0.079	49	0.002		

Table 26. Average egg loss rates for significant habitat variables from the factorial analysis of 1994 and 1995 egg loss rates. Data from rocky and boulder substrates only.

			1994 & 1995 Combined, Rocky and Boulder Substrates Only
Wave Exposure	Exposed	-Z	**-0.098**
		SE	0.009
		n	43
	Protected	-Z	**-0.108**
		SE	0.018
		n	10
Year	1994	-Z	**-0.105**
		SE	0.010
		n	21
	1995	-Z	**-0.096**
		SE	0.011
		n	32

Table 27. Average egg loss rates for each depth for the combined years, 1994 and 1995. Data are from the rocky substrate only

			1994 & 1995 Combined, Rocky Substrate Only
Depth	5 ft	-Z	**-0.178**
		SE	0.021
		n	5
	3 ft	-Z	**-0.137**
		SE	0.016
		n	7
	2 ft	-Z	**-0.135**
		SE	--
		n	1
	1 ft	-Z	**-0.110**
		SE	0.017
		n	6
	0 ft	-Z	**-0.073**
		SE	0.025
		n	5
	-1 ft	-Z	**-0.063**
		SE	0.018
		n	6
	-3 ft	-Z	**-0.089**
		SE	0.018
		n	3
	-5 ft	-Z	**-0.034**
		SE	0.027
		n	5
	-10 ft	-Z	**-0.092**
		SE	0.016
		n	3

1.3.7. Combined Montague Island analyses

Because of the significance of the oiled/unoiled variable in the 1990, and combined 1990 and 1991 analyses, combining data from all four years was done only for Montague Island transects. By using this subset of data, egg loss rates from the two locations (previously oiled and unoiled) were not combined. The Montague Island analysis used all rocky and boulder transects from all four years of the egg loss study. In both 1990 and 1991 there were three rocky or boulder transects on Montague Island. In 1994 and 1995 all transects were located on Montague Island, the majority of which occurred on rocky and boulder substrates.

Graphical Analyses

Graphical analyses of the combined data for Montague Island were performed on rocky and boulder data using the same methods as for previous analyses. Egg loss rates at wave-protected transects seem to be higher than those at wave-exposed transects on Montague Island (Figure 38). Although this is a counterintuitive result, it has been consistent throughout most prior analyses.

Egg loss rates for each year were plotted against both depth (Figure 39) and air exposure (Figure 40). It is evident from these graphs that interannual variation is a factor that must be considered when modeling egg loss, since egg loss rates differed among years.

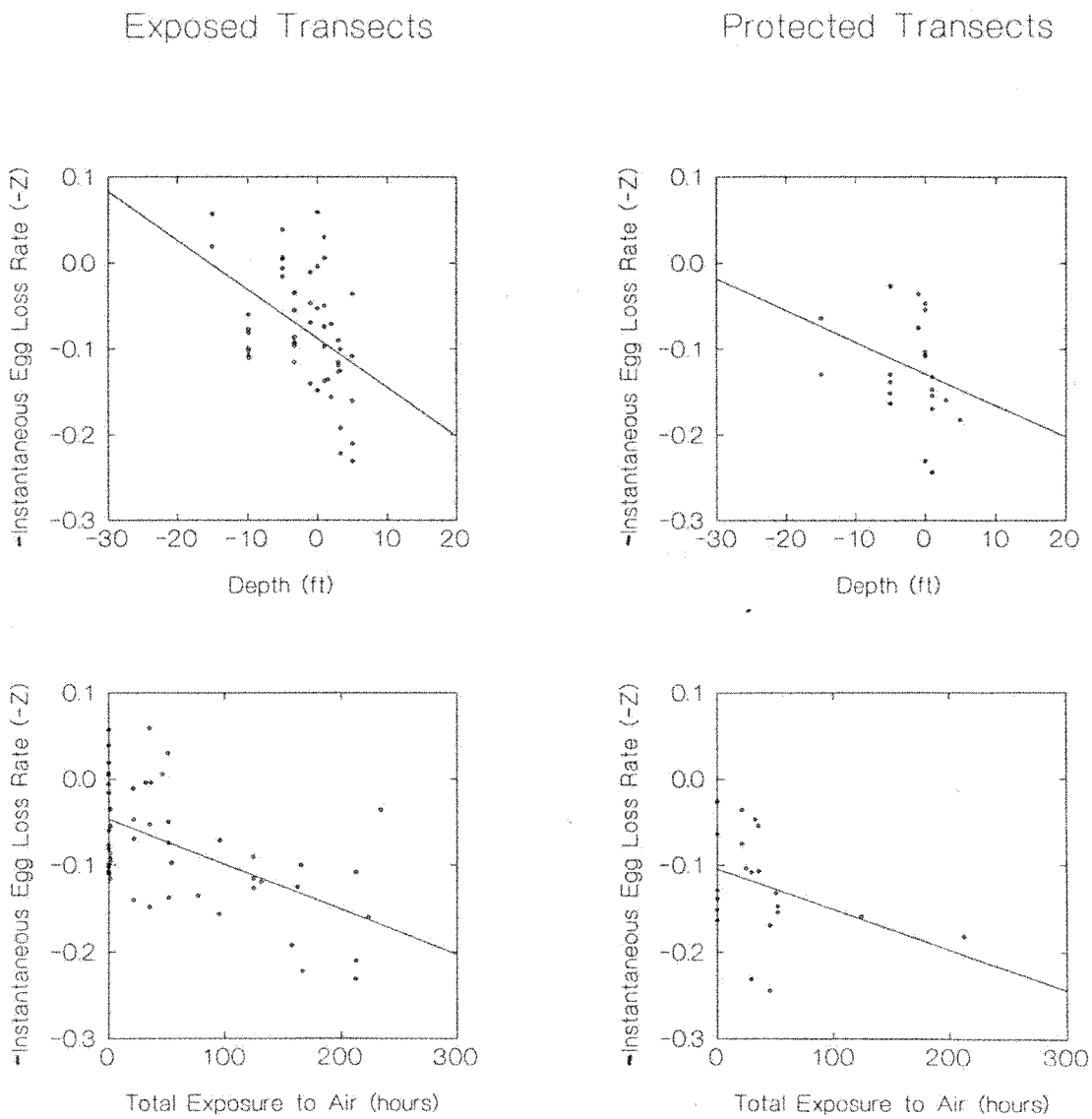


Figure 38. Egg loss rates for wave-exposed and wave-protected transects on Montague Island. Egg loss rates are plotted against both depth and air exposure. Data taken from all years, on rocky and boulder substrates only.

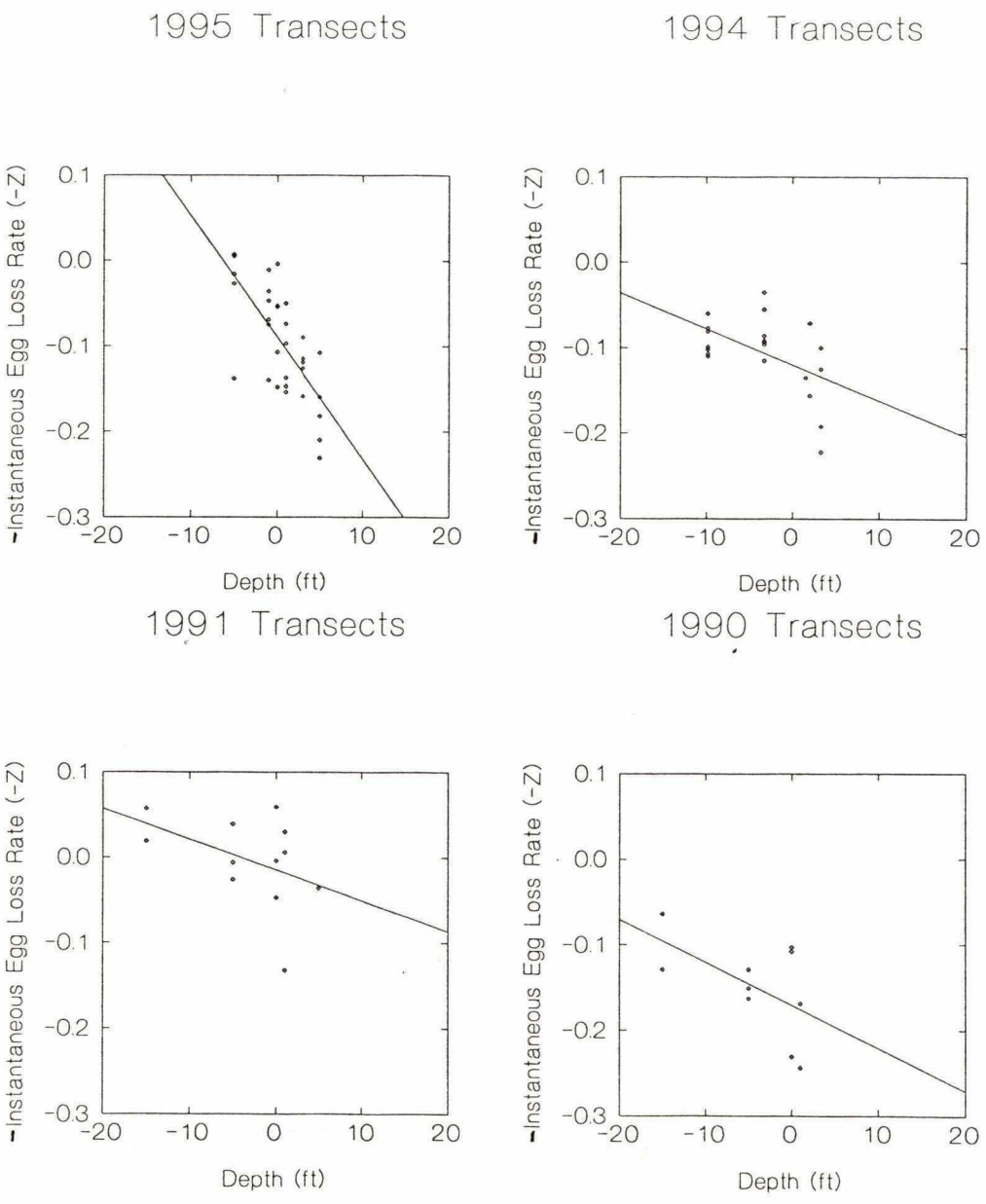


Figure 39. Egg loss rates from Montague Island transects for each year against depth. Data taken from rocky and boulder transects only.

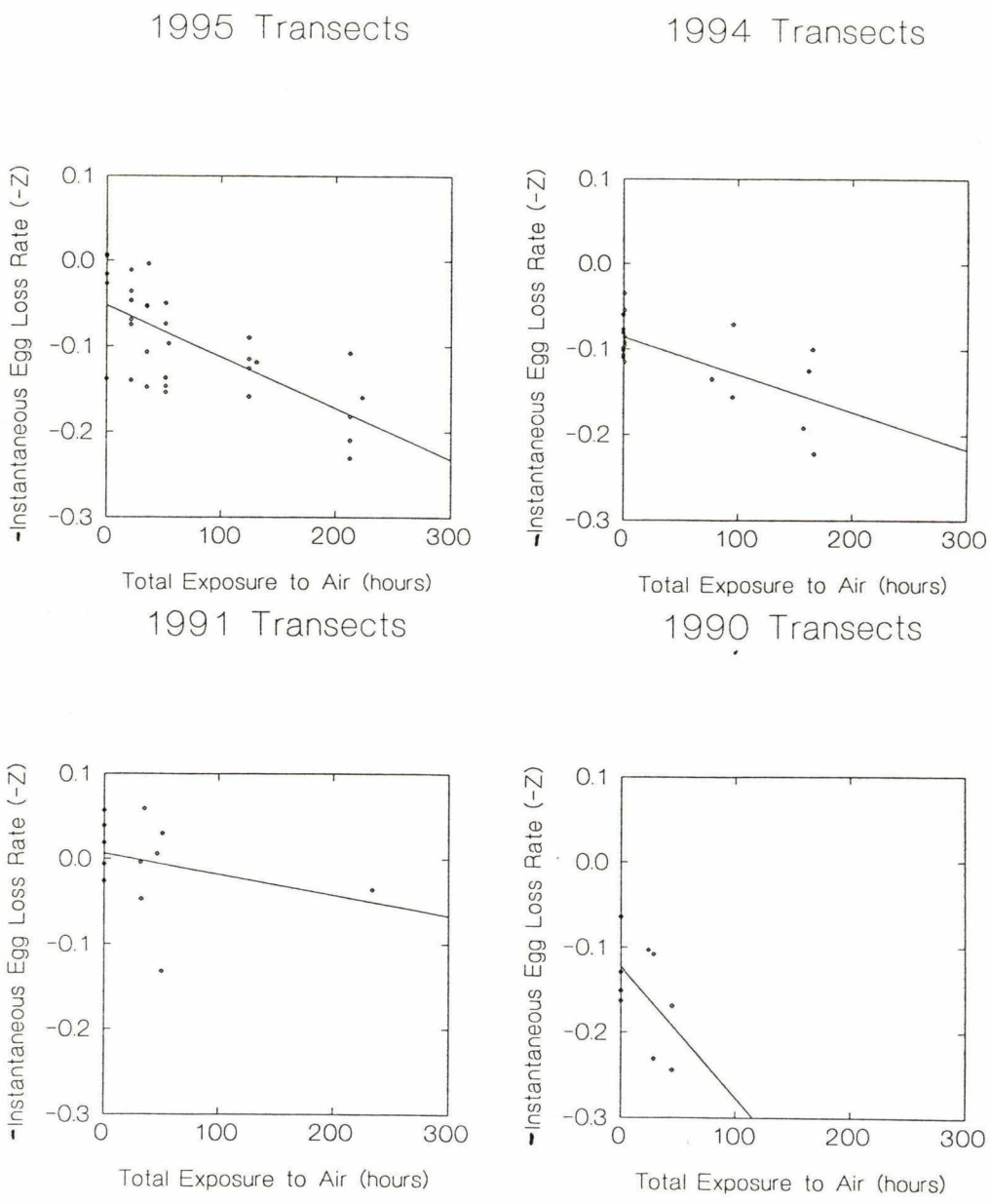


Figure 40. Egg loss rates at transects on Montague Island from each year against air exposure. Data from rocky and boulder transects only.

A plot of egg loss rates against depth and air exposure reveals that egg loss may be higher where large brown kelp is not dominant (Figure 41). However, since this category occurs mainly at the higher depths it is unclear which effect is being seen, the effect of kelp type or the effect of depth.

The final habitat variable used in the analysis of transects occurring on Montague Island was depth. Egg loss rates are lower at deeper depths and lower times of air exposure, which is consistent with all previous results (Figure 42).

Analysis of Covariance

The first step in the statistical analysis of the combined Montague Island egg loss data was to perform an analysis of covariance on data from rocky and boulder transects only, with ln(egg abundance) and days since spawn as the dependent and covariate terms respectively. I included all possible habitat variables and interactions in the analysis, resulting in a model explaining 48.1% of the variability in ln(egg abundance) (Table 28). All the individual habitat variables were significant in the analysis, except kelp type and substrate type. Days since spawn explained the most variability in ln(egg abundance), followed by the depth variable. Only about half of the interaction terms were significant, with the majority of the significant terms being covariate interactions.

Factorial Analyses

Factorial analysis of the combined Montague Island data from only the rocky substrate resulted in a model explaining 71.5% of the variability in egg loss rates (Table

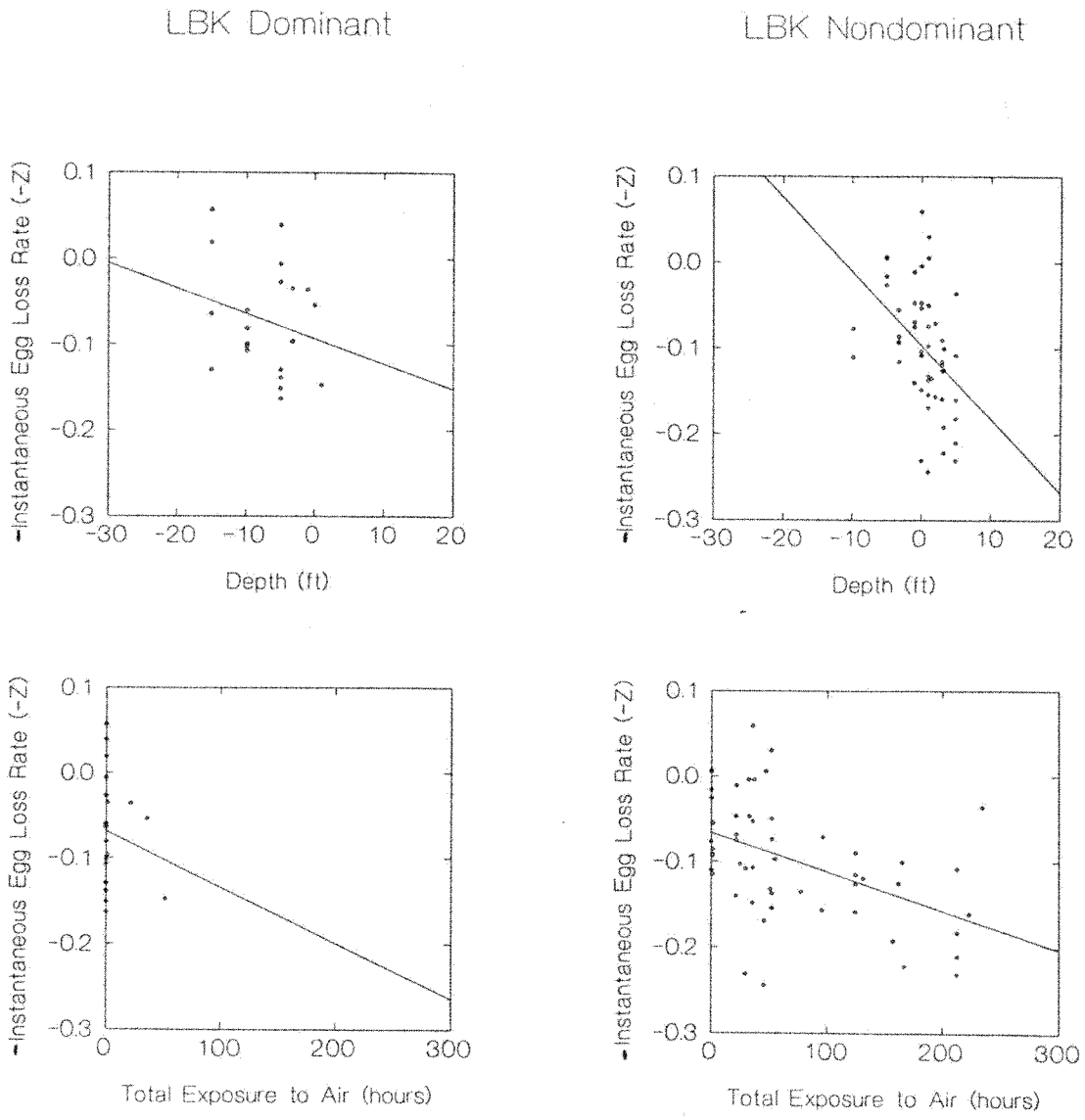
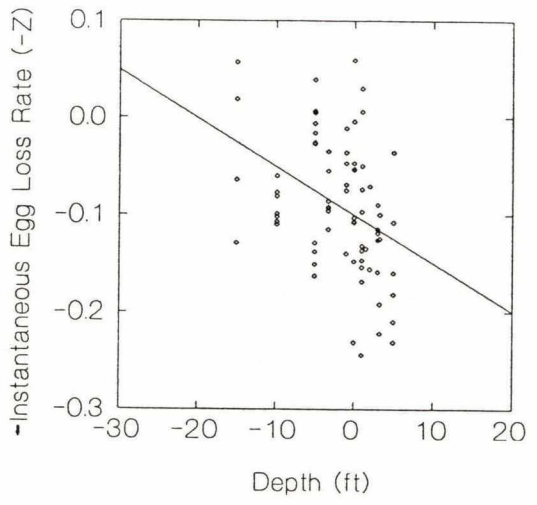


Figure 41. Egg loss rates from Montague Island in each kelp type category. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK) species, and LBK non-dominant refers to quadrats dominated by other vegetation types. Data plotted against both depth and air exposure, and taken from rocky and boulder transects only.



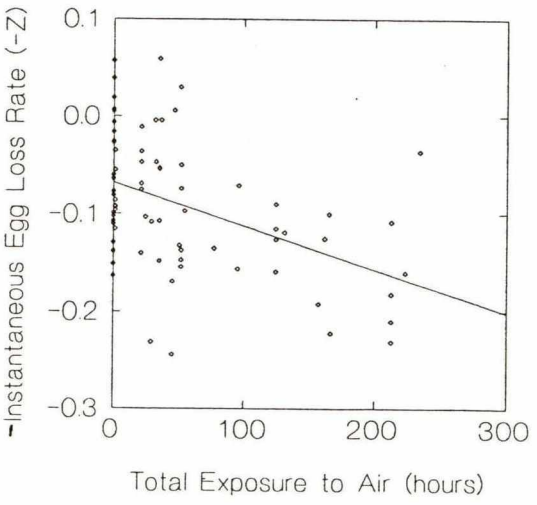


Figure 42. Egg loss rates from Montague Island transects against depth and air exposure. Data taken from all years, rocky and boulder substrates only.

Table 28. Results of analysis of covariance of Montague Island ln(egg abundance) data. Data from rocky and boulder substrates only.

Analysis of Covariance

Dependent Variable: Ln(egg abundance)

n: 2432 Multiple R: 0.694 Squared Multiple R: 0.481

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Wave exposure*Days	0.409	1	0.409	0.193	0.660
Kelp type*Year*Days	25.283	3	8.428	3.981	0.008
Kelp type*Substrate type*Days	9.404	1	9.404	4.443	0.035
Year*Days	44.651	3	14.884	7.031	0.000
Substrate type*Days	7.709	1	7.709	3.641	0.056
Kelp type*Days	22.439	1	22.439	10.600	0.001
Wave exposure*Days	1.543	1	1.543	0.729	0.393
Depth*Days	137.732	9	15.304	7.229	0.000
Kelp type*Wave exposure	0.412	1	0.412	0.195	0.659
Kelp type*Year	22.216	3	7.405	3.498	0.015
Kelp type*Substrate type	4.007	1	4.007	1.893	0.169
Year	51.806	3	17.269	8.158	0.000
Substrate type	0.889	1	0.889	0.420	0.517
Kelp type	0.130	1	0.130	0.061	0.805
Wave exposure	35.715	1	35.715	16.872	0.000
Depth	163.882	9	18.209	8.602	0.000
Days since spawn	233.439	1	233.439	110.493	0.000
Error	5059.299	2390	2.117		

29). It contained three significant terms: depth, wave exposure, and year, with depth explaining the majority of the variation in egg loss rates.

A model of egg loss rates with air exposure in place of depth from data collected at rocky transects only, explained 67.2% of the variability in egg loss rates (Table 30). Year explained the most variation in egg loss rates in this model. Other significant variables were wave exposure and the covariate term, air exposure.

The average egg loss rate for the Montague Island combined data is higher in areas protected from waves (-Z=-0.116 SE=0.015) than in exposed areas (-Z=-0.071 SE=0.012) (Table 31). The year with the highest egg loss on Montague Island was 1990 (-Z=-0.154, SE=0.029), and the following year had the lowest average egg loss (-Z=-0.003, SE=0.015). At deeper depths egg loss rates were lower, a consistent pattern within all the egg loss data (Table 32).

1.3.8. Kelp type analysis

From the previous graphical analyses as well as the factorial analyses, it is apparent that the kelp type variable is confounded with the depth variable. Since large brown kelp is dominant only at subtidal depths, the effect of kelp type cannot be accurately assessed by examining the entire data set. For this reason an additional analysis was performed to directly compare egg loss rates between the large brown kelp dominated and nondominated categories.

Table 29. Results of factorial analysis of Montague Island egg loss rates. Data from rocky transects only.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 59 Multiple R: 0.845 Squared Multiple R: 0.715

Source	Sum of Squares	DF	MSE	F-Ratio	P
Wave exposure	0.018	1	0.018	8.704	0.005
Year	0.068	3	0.023	11.219	0.000
Depth	0.098	9	0.011	5.365	0.000
Error	0.091	45	0.002		

Table 30. Results of factorial analysis of Montague Island egg loss rates, with air exposure in the place of depth. Data from rocky transects only.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 59 Multiple R: 0.819 Squared Multiple R: 0.672

Source	Sum of Squares	DF	MSE	F-Ratio	P
Wave exposure	0.020	1	0.020	10.275	0.002
Air exposure	0.084	1	0.084	42.416	0.000
Year	0.099	3	0.033	16.731	0.000
Error	0.105	53	0.002		

Table 31. Average egg loss rates for significant habitat variables from factorial analysis of Montague Island data. Data from the rocky substrate only.

			Montague Island Data, Rocky Substrate Only
Wave Exposure	Exposed	-Z	**-0.071**
		SE	0.012
		n	40
	Protected	-Z	**-0.116**
		SE	0.015
		n	19
Year	1990	-Z	**-0.154**
		SE	0.029
		n	6
	1991	-Z	**-0.003**
		SE	0.015
		n	12
	1994	-Z	**-0.114**
		SE	0.016
		n	9
	1995	-Z	**-0.096**
		SE	0.011
		n	32

Table 32. Average egg loss rates for each depth category for Montague Island data. Data from rocky substrate only.

			Montague Island Data, Rocky Substrate Only
Depth	5 ft	-Z	**-0.155**
		SE	0.029
		n	6
	3 ft	-Z	**-0.137**
		SE	0.016
		n	7
	2 ft	-Z	**-0.135**
		SE	--
		n	1
	1 ft	-Z	**-0.100**
		SE	0.026
		n	10
	0 ft	-Z	**-0.069**
		SE	0.026
		n	10
	-1 ft	-Z	**-0.063**
		SE	0.018
		n	6
	-3 ft	-Z	**-0.089**
		SE	0.018
		n	3
	-5 ft	-Z	**-0.044**
		SE	0.022
		n	10
	-10 ft	-Z	**-0.092**
		SE	0.016
		n	3
	-15 ft	-Z	**0.004**
		SE	0.036
		n	3

To directly compare kelp types, all egg loss rates below 1 ft relative to mean low water were selected, and an analysis of variance using only the kelp type variable was performed (Table 33). The results show that there is not a significant difference in egg loss rates at depths dominated by large brown kelp and at stations dominated by other vegetation types. Based on this result it appears that in previous analyses where kelp type was significant, the variable responsible for the significance may have actually been depth.

1.3.9. Air exposure versus depth

Based on the factorial analyses of egg loss models, depth is the most important variable affecting egg loss. The depth variable was included in the best model of egg loss rates for every data set examined. Times of air exposure were calculated for each depth and used as covariate in the factorial analyses, but the resulting models were not as significant as the models including depth. In most cases where depth was included in the best model of egg loss rates, the second best model included the air exposure term instead of depth. To analyze whether there were significant differences between models containing depth and models containing air exposure, the contributions to sum of squares with either depth or air exposure included in the model were compared.

Using the best model for each data set examined, an F-test was performed to determine if the models with depth were significantly different than models with air

Table 33. Analysis of variance of egg loss rates from subtidal depths using kelp type as the only explanatory variable. Depths selected were all deeper than +1 foot relative to mean low water.

Analysis of Variance

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 89 Multiple R: 0.141 Squared Multiple R: 0.020

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type	0.010	1	0.010	1.767	0.187
Error	0.501	87	0.006		

exposure (Table 34). The conclusion was that the models with air exposure were not significantly different than those models using depth (P>0.50). This result was consistent for all data sets except 1990 and 1994.

A significant difference in 1994 was probably the result of the combination of depth categories used. This meant that the depth categories used in the modeling did not represent the true relationship between depth and air exposure, resulting in a significant difference between the depth and air exposure models. In 1990 the lack of permanently secured quadrats may have influenced the results of the test. Since the same patch of eggs were not necessarily measured on every visit, depths may not have been consistent.

The benefit of using air exposure instead of depth is that it eliminates the need to estimate egg loss for each depth category, thus reducing the number of parameters estimated without significantly increasing variation. The air exposure increases exponentially as depth relative to mean low water decreases (Figure 43).

1.3.10. Model comparisons

Analyses of Covariance

The analysis of covariance models using habitat variables were compared to analysis of covariance models using only transect and depth as explanatory variables for each of the seven divisions of ln(egg abundance) data (Table 35). The transect-depth

Table 34. Comparison of residual sums of squares for models including depth and models including air exposure.

Data set	RSS_{depth}	RSS_{air}	df_{depth}	df_{air}	σ^2	Calculated F	F statistic	p-value
1990 data	0.019	0.038	13	17	0.0015	3.25	3.18	0.012
1991 data	0.040	0.043	20	23	0.0020	0.50	3.10	0.939
1994 data	0.032	0.103	19	27	0.0017	5.27	2.48	0.000
1995 data	0.057	0.064	26	30	0.0022	0.80	2.74	0.718
1990 and 1991 data	0.077	0.085	41	45	0.0019	1.06	2.60	0.417
1994 and 1995 data	0.069	0.080	32	39	0.0022	0.73	2.31	0.820
Montague Is. data	0.091	0.105	45	53	0.0020	0.87	2.15	0.689

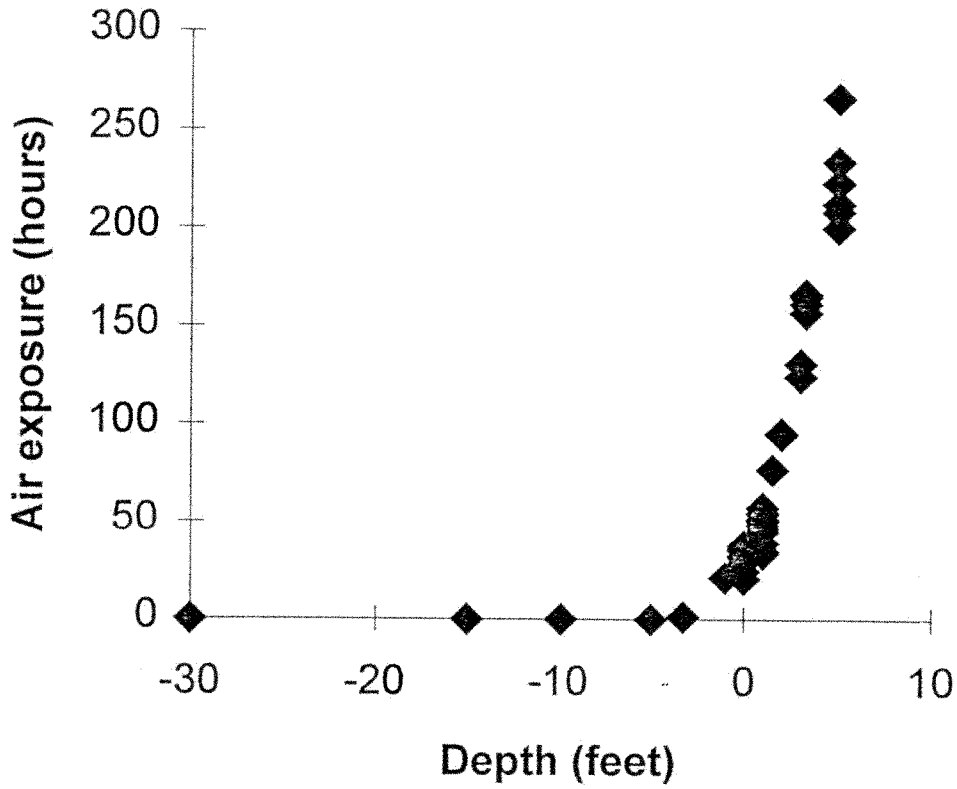


Figure 43. Air exposure against depth. Air exposure is the cumulative exposure, in hours, over the herring egg incubation period at each depth sampled during the egg loss study.

Table 35. Summary of R^2 values for analysis of covariance of ln(egg abundance) data. Models using habitat variables and models using only depth and transect are compared.

Data Set	R^2 for Multiple Habitat Variables	R^2 for Depth & Transect only
1990 data (all substrates)	0.436	0.412
1991 data (rocky only)	0.411	0.476
1994 data (all substrates)	0.406	0.456
1995 data (rocky only)	0.580	0.662
1990 and 1991 data (all substrates)	0.421	0.413
1994 and 1995 data (rocky and boulder only)	0.538	0.628
Montague Is. data (rocky and boulder only)	0.481	0.578
Average	**0.468**	**0.518**
SE	**0.026**	**0.039**

model is equivalent to the model used by Biggs-Brown and Baker (1993) in the analysis of the 1990 and 1991 data. The transect-depth models were consistently better at explaining variability in the data than the models containing only habitat variables (Figure 44). The average R^2 value for the transect-depth models is 0.518 (SE=0.039) while for habitat variable models the average R^2 value is 0.468 (SE=0.026). This result is not surprising since the transect-depth models had many more parameters.

Factorial Analyses

To compare R^2 values from the different modeling techniques, the best habitat models were averaged across each egg loss rate data set modeled. This average was compared to average R^2 values across the same data sets from the three simpler models, models containing the depth term only, models containing the air exposure term only, and models containing transect and depth (Figure 45).

The best models from factorial analyses of egg loss rates had R^2 values ranging from 0.524 for 1995 data to 0.854 for 1990 data (Table 36). The models from factorial analyses include different combinations of the habitat variables, and the average R^2 for these habitat models was 0.679 (SE=0.044).

Models using only depth as an explanatory variable for egg loss rates had an average R^2 of 0.344 (SE=0.057) (Table 37). This is a relatively low average R^2 when compared to the habitat variable models. The low average R^2 may not entirely reflect the strength of depth as an explanatory variable. In 1990 and 1991 differences in egg loss

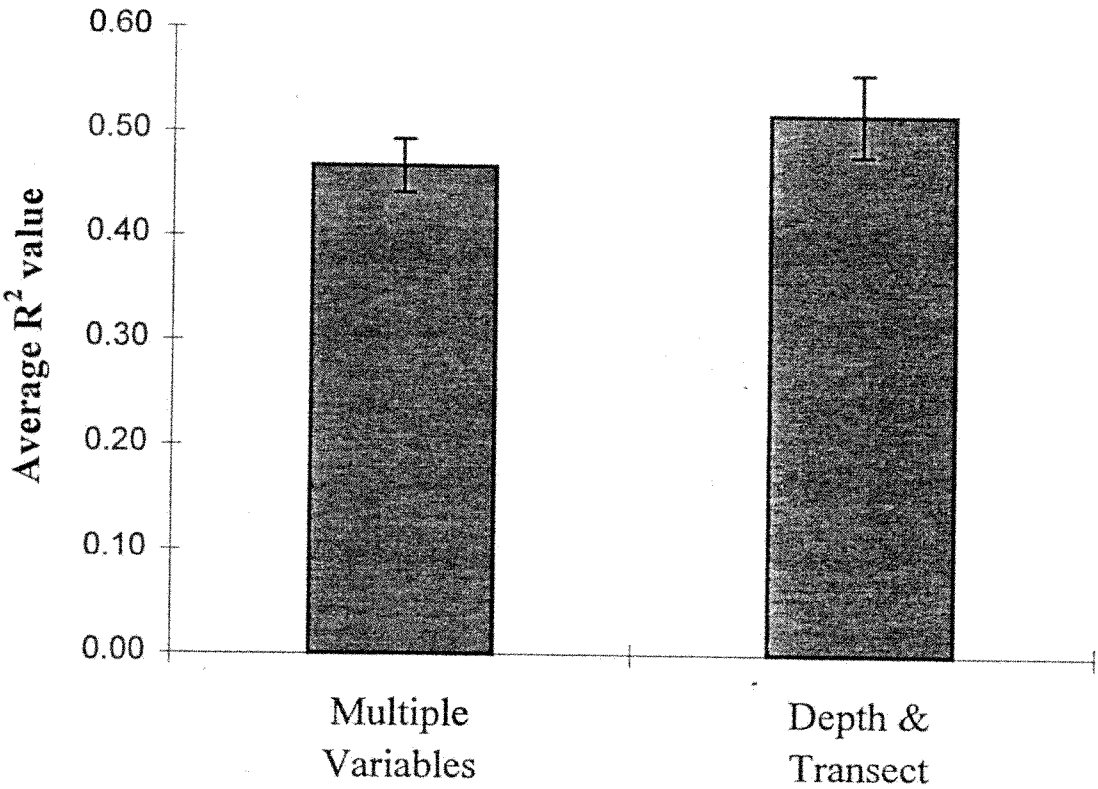


Figure 44. Average R^2 values for analyses of covariance models. The graph shows models with habitat variables, and models with transect and depth only.

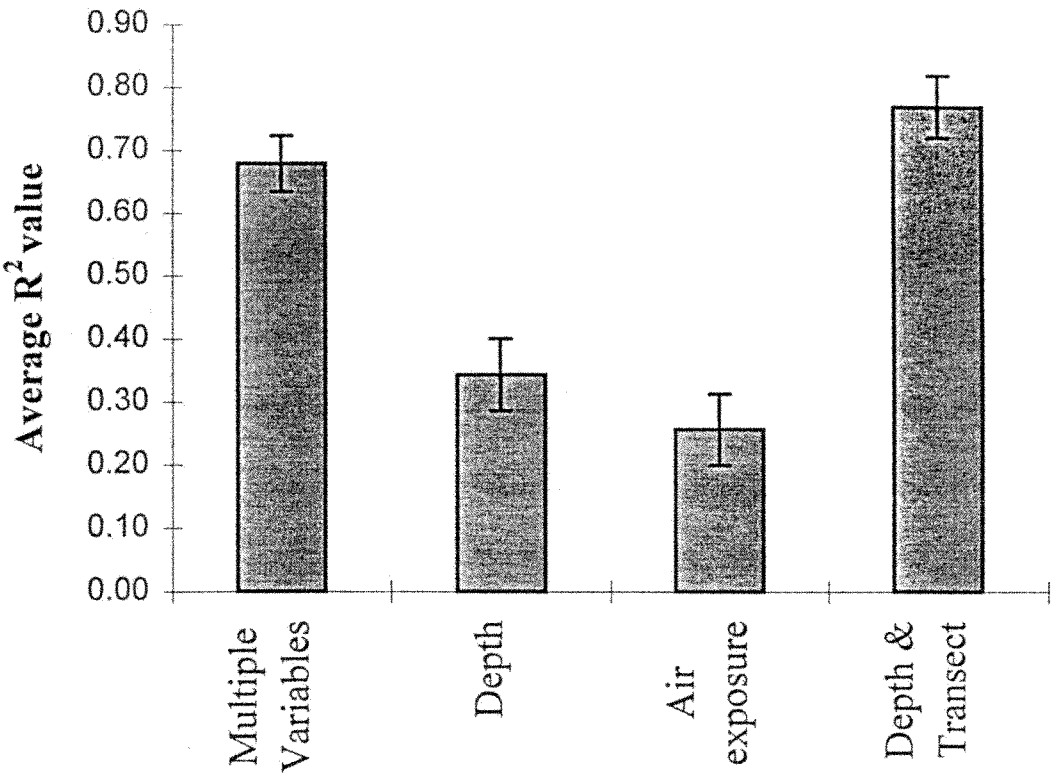


Figure 45. Average R^2 values for analysis of variance models. Each bar represents the average R^2 value for different modeling techniques for comparison.

Table 36. Summary of R^2 values for the models of egg loss rates resulting from factorial analyses of each data set.

Data Set	Habitat variables contained in model	R^2
1990 data (rocky only)	Oiled/unoiled Wave exposure Depth	**0.854**
1991 data (rocky only)	Wave exposure Depth	**0.653**
1994 data (all substrates)	Bird*depth Depth	**0.736**
1995 data (rocky only)	Depth	**0.539**
1990 and 1991 data (rocky and boulder only)	Year*oiled/unoiled Oiled/unoiled Wave exposure Depth Year	**0.734**
1994 and 1995 data (rocky data only)	Depth	**0.524**
Montague Is. data (rocky data only)	Year Wave exposure Depth	**0.715**
	Average	**0.679**
	SE	**0.041**

Table 37. Summary of R^2 values for each data set for models of egg loss rates containing only depth as an explanatory variable.

Data Set	Habitat variable contained in model	R^2
1990 data (rocky only)	Depth	**0.418**
1991 data (rocky only)	Depth	**0.227**
1994 data (all data)	Depth	**0.211**
1995 data (rocky only)	Depth	**0.539**
1990 and 1991 data (rocky and boulder only)	Depth	**0.178**
1994 and 1995 data (rocky data only)	Depth	**0.524**
Montague Is. data (rocky data only)	Depth	**0.308**
	Average	**0.344**
	SE	**0.057**

rates between oiled and unoiled areas, and between the two years were more important, therefore the R^2 values for models including only depth are low. In 1994 and 1995 the R^2 values for models including only depth were high, and for both 1995 and the combined 1994 and 1995 data, models containing only depth resulted from the factorial analyses of all habitat variables (Table 36). When average R^2 values were compared for the four types of models for 1994, 1995 and both years combined, models containing only depth and only air exposure were much closer to the other two types of models (Figure 46).

Models containing only air exposure also had a fairly low average R^2 value of 0.257 with a standard error of 0.056 (Table 38). As in the case for models containing only depth, this low value also reflects the differences between the two sets of years (1990-1991 and 1994-1995).

Models containing only depth and transect explained the most variability of all the models examined (Table 39). The average R^2 value for these models over all the egg loss rate data sets examined was 0.769 (SE=0.049).

1.4. Discussion

Some major differences between the first two years of the study, 1990 and 1991, and the last two years, 1994 and 1995, are evident from the egg loss models. In the later years depth seems to be the most important environmental variable driving egg loss in

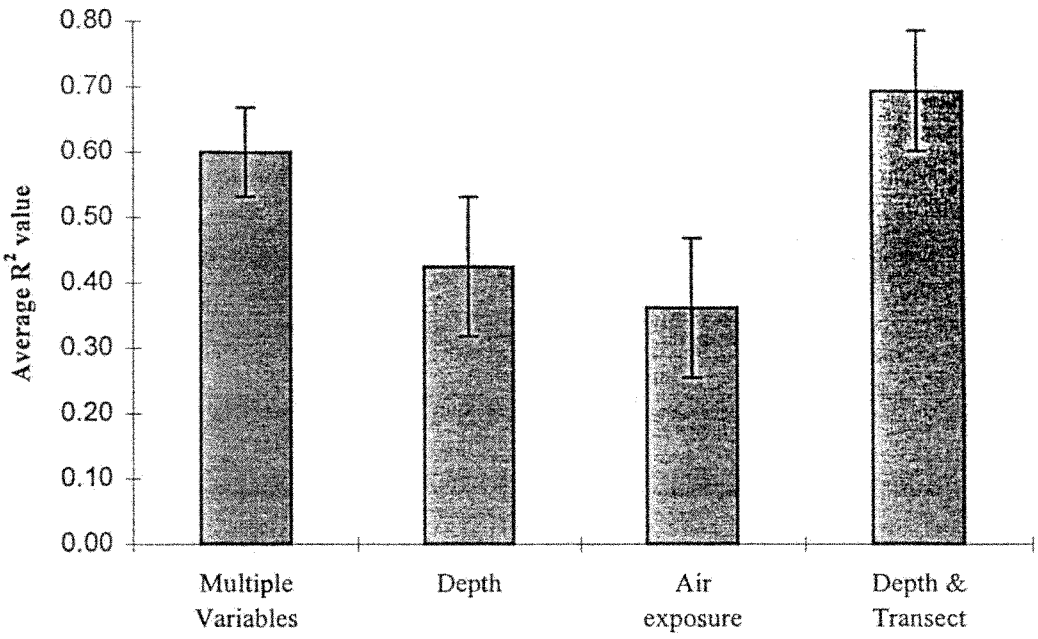


Figure 46. Average R^2 values for analysis of variance models for 1994 and 1995 only. Models using different explanatory variables are represented by each bar.

Table 38. Summary of R^2 values for each data set for models of egg loss rates containing only air exposure as an explanatory variable.

Data Set	Habitat variables contained in model	R^2
1990 data (rocky only)	Air exposure	**0.189**
1991 data (rocky only)	Air exposure	**0.181**
1994 data (all substrates)	Air exposure	**0.149**
1995 data (rocky only)	Air exposure	**0.486**
1990 and 1991 data (rocky and boulder only)	Air exposure	**0.118**
1994 and 1995 data (rocky data only)	Air exposure	**0.451**
Montague Is. data (rocky data only)	Air exposure	**0.222**
	Average	**0.257**
	SE	**0.056**

Table 39. Summary of R^2 values for each data set for models of egg loss rates containing transect and depth as explanatory variables.

Data Set	Habitat variables contained in model	R^2
1990 data (rocky only)	Depth Transect	**0.921**
1991 data (rocky only)	Depth Transect	**0.716**
1994 data (all substrates)	Depth Transect	**0.512**
1995 data (rocky only)	Depth Transect	**0.800**
1990 and 1991 data (rocky and boulder only)	Depth Transect	**0.807**
1994 and 1995 data (rocky data only)	Depth Transect	**0.776**
Montague Is. data (rocky data only)	Depth Transect	**0.854**
	Average	**0.769**
	SE	**0.052**

Prince William Sound, while in the early years a combination of variables including depth were significant. There were some differences between the two sets of years which may be related to this result. Spawning biomass was higher in the early years than the later years, which may have affected egg loss. The 1990 and 1991 data is from a wide range of locations in Prince William Sound, while the 1994 and 1995 data is from Montague Island only. Thus, egg loss may be influenced by depth within each location, but sound-wide patterns in egg loss may be strongly influenced by the different conditions experienced in each area. This seems to be true from examination of the egg loss model for Montague Island transects only. This data set included all years, but was limited to a fairly small range of locations, and indeed depth proved to be the most significant factor in the model.

It is apparent that depth is probably the most important variable affecting egg loss. It was included in all factorial analyses of egg loss, and was the predominant variable in the models of 1994 and 1995 data. Air exposure is a good substitute for depth, reducing the number of parameters estimated without significantly decreasing the efficiency of the model.

The wave exposure variable produced a very interesting result in that egg loss was consistently higher at protected transects than at exposed transects. The only year where egg loss was higher at exposed transects was 1990, and in this year the wave-exposed category was represented by only one transect. Lower egg loss in exposed areas is highly

counter-intuitive and may reflect the presence of an undiscovered process driving egg loss in protected areas. Examination of data collected by wave sensors placed at three egg loss transects in 1995 indicate there may be a threshold wave energy level (Chapter 3). Beyond this threshold wave forces may result in high levels of egg loss, while below this threshold energy level egg loss due to wave energy may be negligible.

Both substrate type and kelp type were found to be insignificant in most models of egg loss rates. Substrates other than rocky were not well represented in most years, so replication was not sufficient to provide robust analyses. The kelp type variable was confounded with the depth variable since large brown kelp typically did not occur at depths above mean low water. The analysis of egg loss rates to address the problem of kelp type indicated that kelp type was highly insignificant in predicting the rate of egg loss.

Oiled/unoiled condition (location) was very important, especially in 1990. The differences in physical and biological regimes between the north and south sound are probably responsible for the differences in observed egg loss between the two areas. In 1991 the differences in egg loss rates between oiled and unoiled locations was not significant, suggesting the physical and biological regimes in the two areas were more similar in 1991 than in 1990. In 1994 and 1995 this variable was not examined since the majority of spawn was located in the south sound at Montague Island.

Of the covariate terms used in the modeling (average bird abundance, average gull abundance, the fish predation index and cumulative loose eggs), only bird abundance was significant, and only in 1994, when increased bird abundance resulted in higher egg loss rates. Predator exclusion experiments were conducted at egg loss transects in 1994 and 1995, the results of which are summarized in Appendix C of Rooper et al (1996). These experiments showed that there was no significant effect of birds on egg loss, but this may have been caused by the failure of the exclusion cages to function correctly. These results suggest that predation was a relatively unimportant process driving egg loss in Prince William Sound.

The "Avian Predation on Spawn" study carried out by the US Forest Service (C.R.D.I.) estimated that birds removed 19.24% of the total herring spawn in an area of Montague Island, quite a large percentage. The reason for the conflicting results may lie in the choice of predator indices used in egg loss modeling. For modeling, the average abundance of predators was used as a covariate; however, this failed to account for the total abundance of spawn at the egg loss transect. Thus, the consumption of eggs by a lesser number of predators at a transect with low egg density would result in a higher egg loss rate than the consumption by many predators at a transect with large numbers of eggs. This would explain the inverse relationship between predators and egg loss rates found in 1995 for both fish and birds, and still allow predation to be an important process regulating egg loss.

Parameters for models with depth and air exposure models were estimated for each egg loss rate data set (Table 40). The model of egg loss recommended by this study is based on the air exposure over the incubation period. The assumption of this approach is that the rate of egg loss is linearly related to air exposure. Our results did not reveal any violation of this assumption. Using the time of air exposure from each depth where spawn is estimated during spawn deposition surveys, it is possible to estimate the rate of egg loss at that depth and thus the number of eggs initially spawned for each observation. This eliminates the need for a blanket estimate of an egg loss correction factor, such as the 10% value used for previous biomass estimates. Instead, the biomass of spawning herring can be directly estimated from the spawn deposition data itself.

Interannual variation in the strength of other habitat variables may increase or decrease their contribution to herring egg loss causing them to become significant, as was seen with the oiled/unoiled term in 1990. An air exposure based model will account for a significant proportion of egg loss in most years, without having to include transect based variation.

Table 40. Parameter estimates of depth and air exposure models for each data set.

Data Set	Egg Loss Rates at Depth		Air exposure parameters	
	Depth	-Z (SE)		
1990 data (rocky only)	-30	0.002 (0.005)	Constant (SE)	-0.0568 (0.0184)
	-15	-0.015 (0.022)	Slope (SE)	-0.0006 (0.0003)
	-5	-0.056 (0.035)		
	0	-0.112 (0.034)		
	1	-0.126 (0.043)		
	5	-0.171 (---)		
1991 data (rocky only)	-15	-0.026 (-0.029)	Constant (SE)	0.0238 (0.0147)
	-5	-0.015 (0.012)	Slope (SE)	0.0004 (0.0002)
	0	-0.038 (0.025)		
	1	-0.046 (0.025)		
	5	-0.124 (0.074)		
1994 data (all substrates)	-10	-0.086 (0.009)	Constant (SE)	0.0809 (0.0130)
	-3	-0.090 (0.012)	Slope (SE)	0.0004 (0.0002)
	-2	-0.058 (0.044)		
	0	-0.064 (0.102)		
	2	-0.121 (0.026)		
	3	-0.160 (0.028)		
1995 data (rocky only)	-5	-0.034 (0.027)	Constant (SE)	0.0524 (0.0115)
	-1	-0.063 (0.018)	Slope (SE)	0.0006 (0.0001)
	0	-0.073 (0.025)		
	1	-0.110 (0.017)		
	3	-0.122 (0.011)		
	5	-0.178 (0.021)		

Table 40 (continued). Parameter estimates of depth and air exposure models for each data set.

Data Set	Egg Loss Rates at Depth		Air exposure parameters	
	Depth	-Z (SE)		
1990 and 1991 data (rocky and boulder only)	-30	0.002 (0.005)	Constant (SE)	0.0530 (0.0100)
	-15	-0.032 (0.019)	Slope (SE)	0.0003 (0.0001)
	-5	-0.044 (0.019)		
	0	-0.074 (0.021)		
	1	-0.087 (0.024)		
	5	-0.136 (0.051)		
1994 and 1995 data (rocky data only)	-10	-0.092 (0.016)	Constant (SE)	0.0683 (0.0078)
	-5	-0.034 (0.027)	Slope (SE)	0.0005 (0.0001)
	-3	-0.089 (0.018)		
	-1	-0.063 (0.018)		
	0	-0.073 (0.025)		
	1	-0.110 (0.017)		
	2	-0.135 (---)		
	3	-0.137 (0.016)		
	5	-0.178 (0.021)		
Montague Is. data (rocky data only)	-15	0.004 (0.036)	Constant (SE)	0.0676 (0.0092)
	-10	-0.092 (0.016)	Slope (SE)	0.0004 (0.0001)
	-5	-0.044 (0.022)		
	-3	-0.089 (0.018)		
	-1	-0.063 (0.018)		
	0	-0.069 (0.026)		
	1	-0.100 (0.026)		
	2	-0.135 (---)		
	3	-0.137 (0.016)		
	5	-0.155 (0.029)		

Chapter 2. Calculations of egg loss at selected 1995 transects.

2.1. Introduction

One of reasons for studying egg loss for Prince William Sound herring is that the population biomass is annually calculated using the number of eggs spawned. The number of eggs spawned is estimated for Prince William Sound by dive surveys at randomly located transects throughout the spawning beds. Since the survey cannot be conducted until some time after spawning, egg loss must be accounted for. As mentioned previously a correction factor of 10% has been used in the past, and from the 1990 and 1991 egg loss data Biggs-Brown and Baker (1993) determined a range of correction factors from 10 to 15% for Prince William Sound. They also estimated that the total loss of eggs from the beginning of spawning until hatching ranged from 50% to 91%.

One of the objectives of the 1995 egg loss sampling was to estimate the correction factor and the total loss of eggs using the egg loss model developed for Prince William Sound. Rather than compute these for the egg loss transect itself, a spawn deposition transect was used. Egg loss transects do not reflect the gradient of the spawning bed, or the distribution of eggs at each depth; they are just snapshots of egg loss occurring at each depth where quadrats were installed. They do not tell us how many eggs were deposited

in the area at that depth, nor the total number of eggs lost for the area. To accomplish this a spawn deposition transect must be used.

2.2. Materials and Methods

To accurately represent the depth distribution and total abundance of spawn, a spawn deposition transect was placed at the same location as each egg loss transect in 1995. Divers counted eggs along a transect extending perpendicular from the beach, continuing past the depth at which no more spawned eggs were observed. The data collected were estimates of the number of eggs in 0.1 m^2 quadrats at 5 meter intervals along the transect.

The model of egg loss developed for Prince William Sound (Chapter 1) was then used to calculate the total number of eggs initially deposited at these transects, as well as the number of eggs retained until hatching at the transect. In 1995 the best model of egg loss included only the depth term, which was replaced by air exposure since this variable estimates fewer parameters.

From examination of air exposure at each depth from 1995 egg loss transects, it is evident that the square root of the time of air exposure is a linear function of depth, (Figure 47). Thus, for depths above -3.5 feet, air exposure in 1995 was calculated using the relationship,

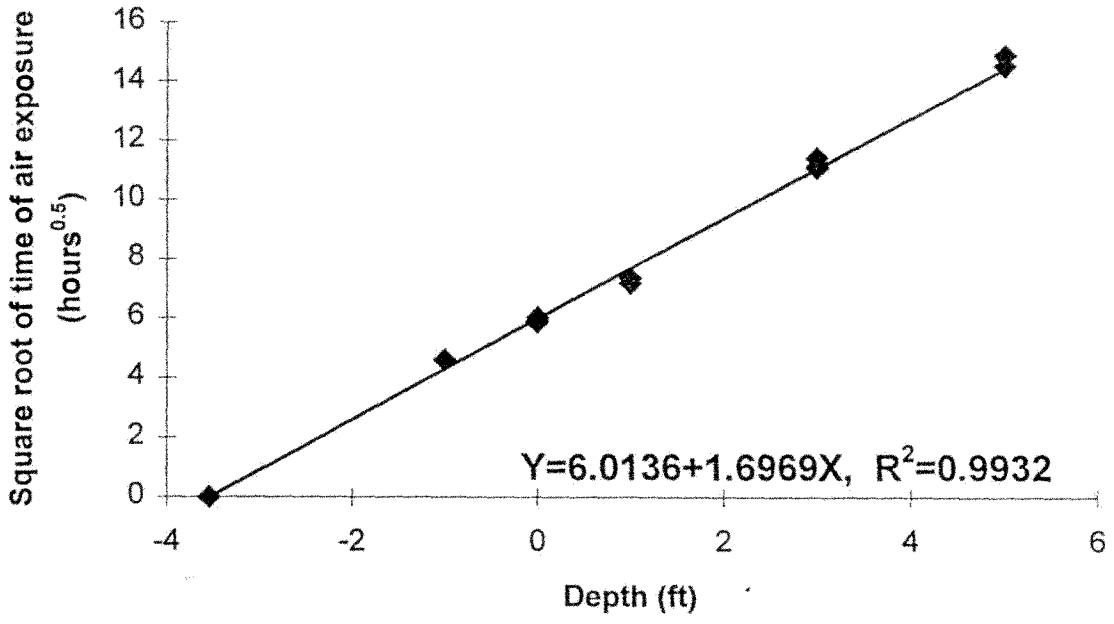


Figure 47. Regression of the square root of air exposure and depth for 1995.

$$AE=(6.013697+1.696911*D)^2 \quad (1)$$

where AE is air exposure over incubation in hours and D is depth in feet. All depths below -3.5 feet were not exposed to air during incubation, thus AE is equal to zero.

The egg loss rate for each depth where eggs were counted during spawn deposition surveys was calculated using the equation

$$Z=0.052357+0.000601*AE \quad (2)$$

from the linear relationship shown in Figure 24. The number of eggs observed at the time of the spawn deposition survey is

$$N_t=N_0e^{-Zt}, \quad (3)$$

where t is the time in days since spawning occurred. Thus, the initial number of eggs deposited, N_0, is

$$N_0=N_te^{Zt} \quad (4)$$

where Z is calculated from (2).

2.3. Results.

In 1995 the beginning of spawning ranged from May 27 to May 29, with spawning at most transects beginning on May 28. The average time from beginning of spawning to spawn deposition survey was 4.9 days, with a range from 4 to 7 days. The

average time of the incubation period in 1995 was 21.1 days, with a range of 21 to 22 days.

Based on the model, the average percent eggs lost from the time of spawning to the time at which the spawn deposition survey took place was 6.67% per day. This value increased from 4.61% per day at subtidal depths to 18.96% per day at higher depths (Figure 48). The model calculates the average egg loss from the time of spawning to the time of the survey at 33% (SE=1.0%). This value ranges from 18.9% at deeper depths to 89.6% at the highest depths.

The percentage of eggs lost over the entire incubation period ranged from 67.40% at subtidal depths to an asymptote at 100% at the shallower depths (Figure 49). The average percentage of eggs lost over the incubation period was 76.06%. Based on the original egg distribution, the majority of eggs that remained in the spawning beds until hatching were deposited in the region between 0 ft and -10 ft relative to mean low water (Figure 50).

2.4. Discussion.

The average percentage of eggs lost from the time of spawning to the time of the survey in 1995 was calculated at 33%. This value is much higher than the assumed value of 10%, and higher than the range of values from 10 to 15% found by the previous

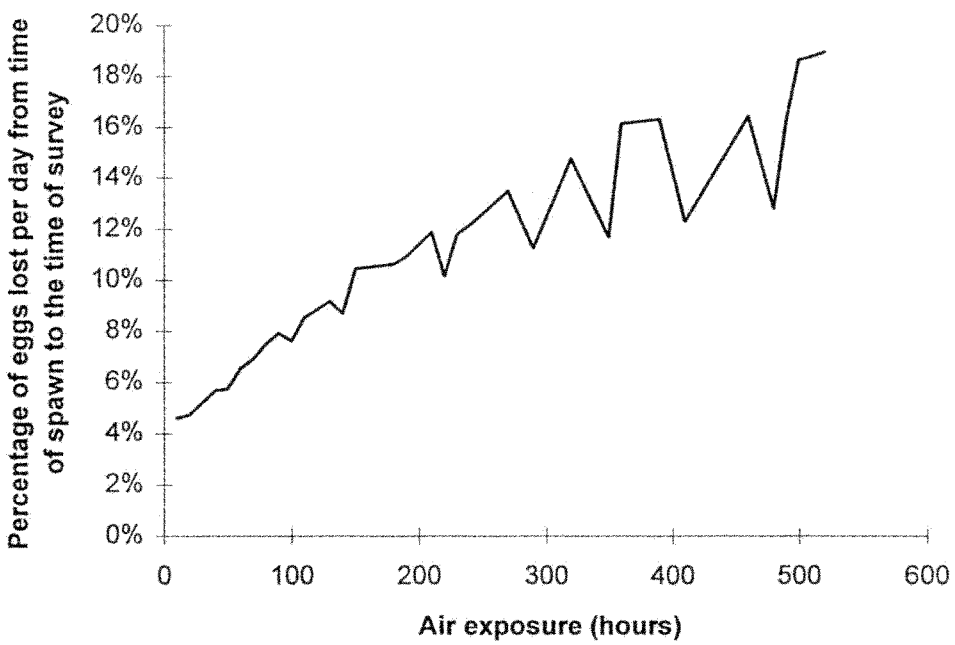


Figure 48. Percentage of eggs lost from time of spawning to time of survey in 1995. Percentages are predicted by the time of air exposure model. Percentages are averaged for ten hour increments of air exposure.

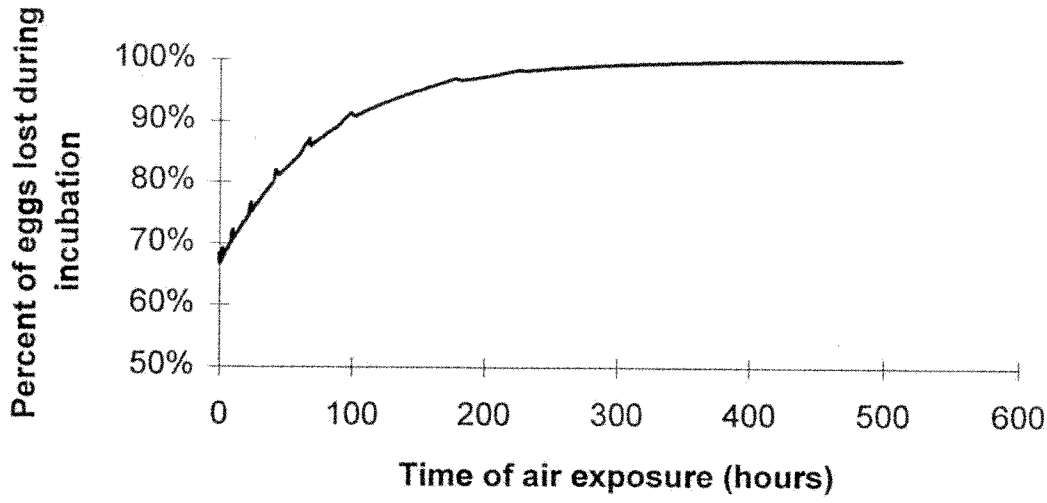


Figure 49. Percentage of eggs lost from time of spawning to time of hatching in 1995. Percentages are predicted for spawn deposition transects by the time of air exposure model. Percentages are averaged for ten hour increments of air exposure.

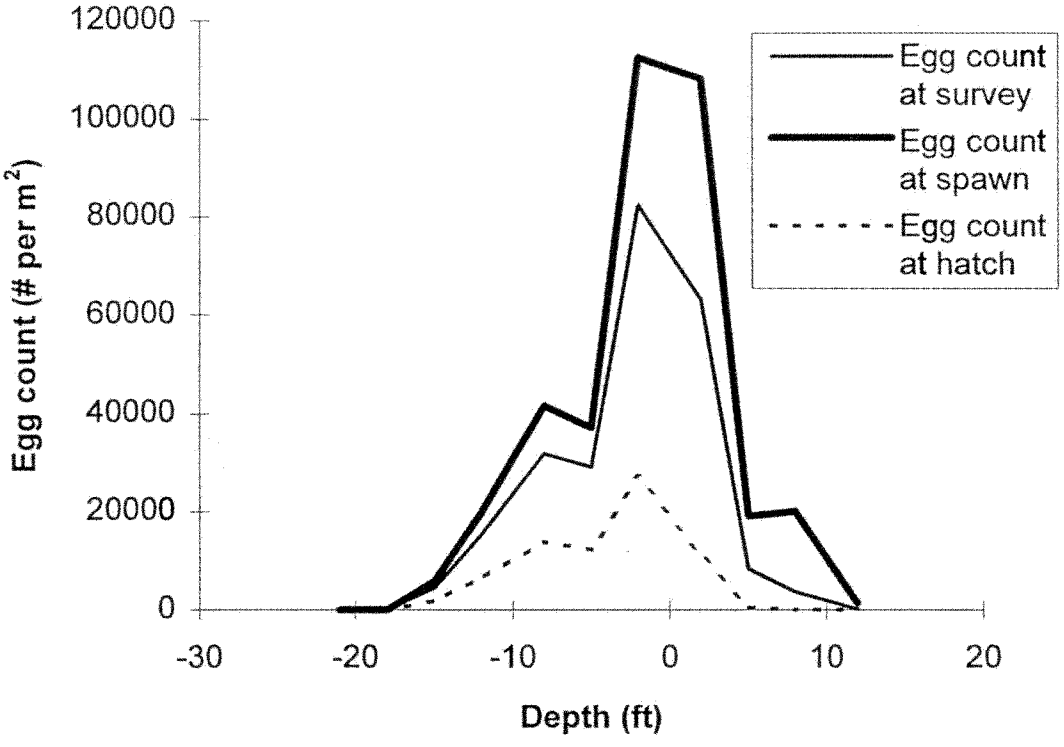


Figure 50. Egg distibution observed at the time of survey, and the number of eggs initially spawned and the number remaining until hatching as predicted by the egg loss model. Data are from selected 1995 transects only.

method (Biggs-Brown and Baker 1993). In the previous evaluation Biggs-Brown and Baker (1993) excluded the highest depth station from their estimate of the correction factor. When that depth is included, their range of eggs lost from spawn to survey increases to 21-38%.

The range of the total percentage of eggs lost over incubation according to the 1995 model (67.4-100%) is slightly higher than the range found by Biggs-Brown and Baker (1993) of 50.4% to 91.2%. Other ranges of total egg loss from Pacific herring spawning beds are from 56-99% for Barkeley Sound, British Columbia (Outram 1959) and from 46-92% for Georgia Strait, British Columbia (Haegele and Schweigert 1991). The results of our model are quite similar to other studies of Pacific herring egg loss, and all studies have found that extremely high egg loss occurs at the highest depths.

It is important to note that the relationship between air exposure and depth changes with both the length of the incubation period and year, since tides will be different from year to year depending on when spawning and hatching occur. For this reason it is important to calculate a new relationship between time of air exposure and depth in each year, specific to the timing and duration of the herring egg incubation period in each year.

Chapter 3. Wave energy analyses.

3.1. Introduction.

The force of wave action has been observed to dislodge Pacific herring eggs in British Columbia creating large windrows of unattached eggs (Hart and Tester 1934; Hay and Miller 1982). Wave action was also believed to cause a substantial proportion of egg loss in Prince William Sound in 1990 and 1991 (Biggs-Brown and Baker 1993). In 1995 sampling was undertaken to measure the effect of wave action on egg abundance at three egg loss transects. Two primary objectives of this portion of the egg loss study were (1) to correlate egg loss between sampling visits with wave energy measurements at the transects, and (2) to provide justification for the wave exposure variable used in the egg loss model (Chapter 1).

3.2. Materials and Methods.

A SEAGAUGE wave and tide recorder (SBE 26-OX) was installed at each of three egg loss sites by an oceanographer from the Prince William Sound Science Center. The recorders provided a continuous measure of wave pressure which was then converted into wave energy (joules$*m^{-2}*day^{-1}$) by a summary program. The installation sites included two

wave-exposed transects, #9 (Graveyard Point) and #6 (Montague Point), as well as one wave-protected transect #2 (inside Rocky Bay).

To assess the effect of wave force on egg loss, I correlated changes in egg abundance between sampling visits to the average wave energy*day^{-1} at each transect during the same time period using analysis of covariance techniques. Wave energy was the covariate predicting changes in egg abundance between visits.

I also compared the mean wave energy at the two wave-exposed transects to the mean wave energy at the wave-protected transect using a paired t-test. This analysis was designed to test the integrity of the wave exposure dummy variable included in the egg loss model. For the wave exposure variable to be considered valid, there must be significant differences in wave energy between the two classifications, wave-exposed and wave-protected. Because of the extremes of wave energy recorded during the incubation period, each observation of wave energy*day^{-1} was ranked and compared between the two classifications using nonparametric methods. This helped to minimize the variance of the observations while preserving the integrity of each observation.

3.3. Results

To directly assess the effect of wave force on egg loss, wave energy was used as a covariate predicting changes in egg abundance during the time interval between transect

visits. Based on the graphical analysis of the data, depth was not included as a categorical predictor, since changes in egg abundance between transect visits seem to exhibit no relationship with depth (Figure 51). It was originally thought that more herring eggs would be lost due to wave action at +5 feet on the beach where eggs would be exposed to breaking waves than at -5 feet where the eggs are submerged.

Changes in egg abundance between sampling visits plotted against average wave energy during the same time period reveals that, as average wave energy*day^{-1} increases, egg loss increases (changes in egg abundance become predominantly negative) (Figure 52). However, the relationship is heavily influenced by the largest average wave energy recorded, 8229 joules*m^{-2}*day^{-1}. The large wave energy value was recorded at transect #6 (Montague Point) only, and marked the occurrence of a large storm event. Large losses of eggs were associated with this wave energy value.

Excluding the largest value, the range of wave energies recorded is from 2 to 561 joules*m^{-2}*day^{-1}. A plot of these smaller wave energies against the corresponding changes in egg abundance reveals no relationship (Figure 53). At these levels of wave energy both egg losses and egg gains were observed, and no real pattern can be discerned.

When wave energy and changes in egg abundance are plotted for each transect against sample date, no clear pattern can be seen in the data, except in the case of the large storm event at transect #6 (Figure 54). Changes in egg abundance and wave energies at transect #6 span a considerably larger range than were recorded at other transects.

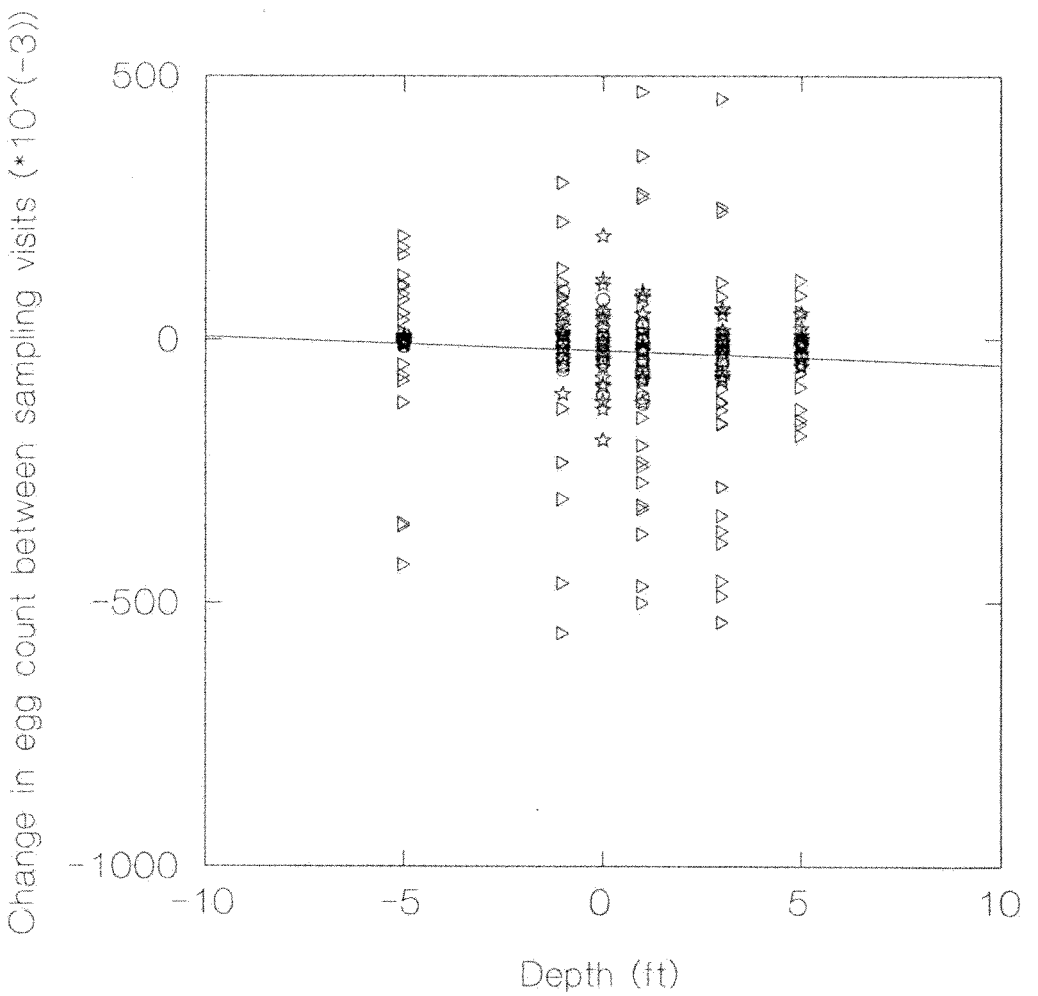


Figure 51. Change in egg abundance (in thousands of eggs) between sampling visits against depth in 1995. Triangles represent transect #6, stars represent transect #9 and circles represent transect #2.

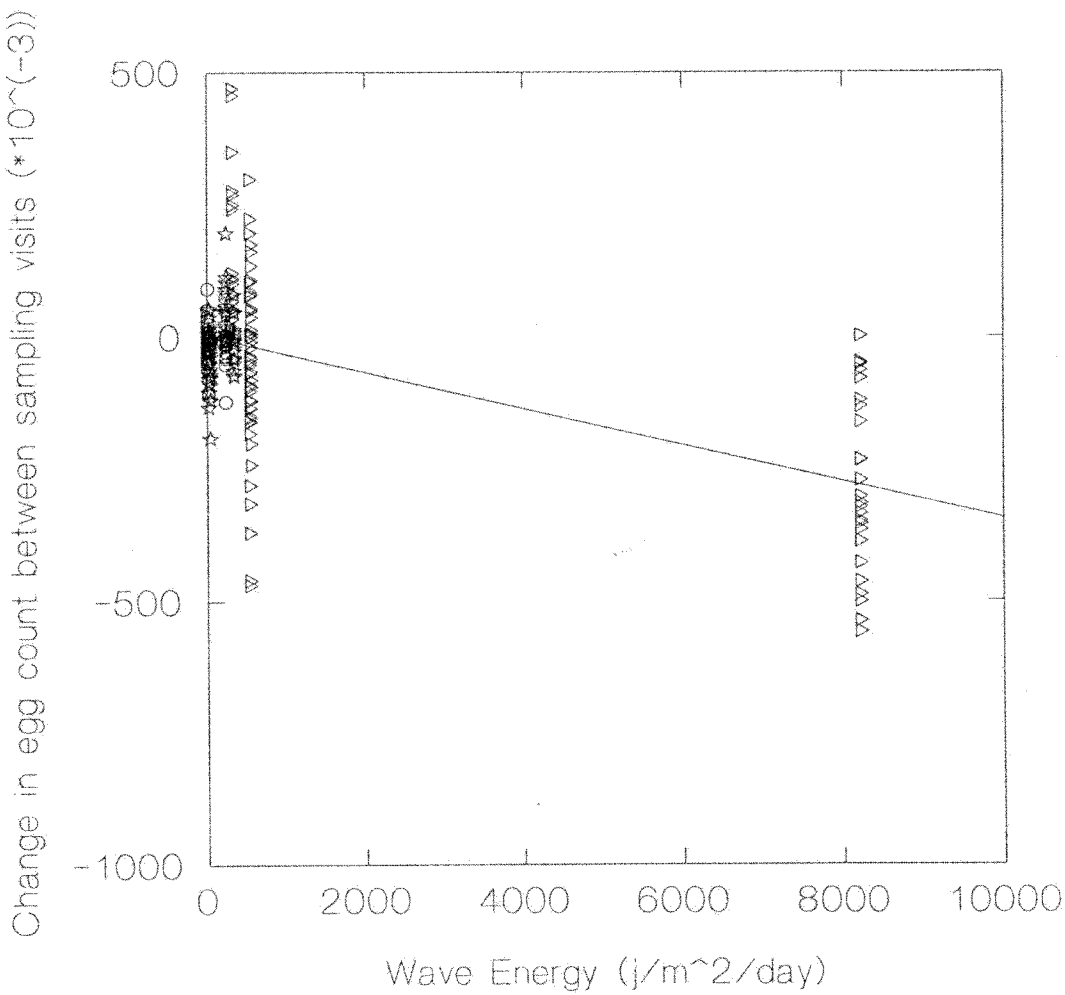


Figure 52. Change in egg abundance (in thousands of eggs) between sampling visits against wave energy. Wave energy per day was measured at three transects by pressure sensors in 1995. Triangles represent transect #6, stars represent transect #9 and circles represent transect #2.

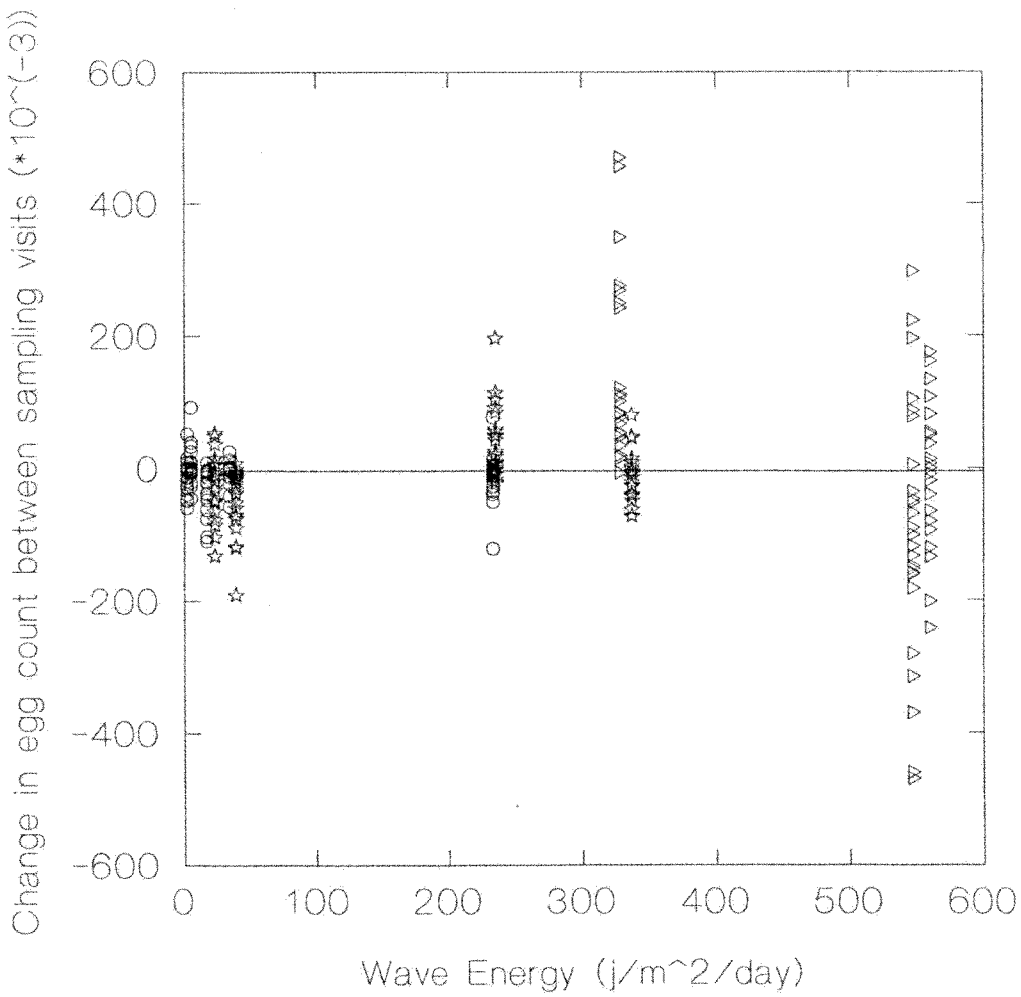


Figure 53. Changes in egg abundance (in thousands of eggs) between sampling visits against wave energies less than 600 $j*m^{-2}*day^{-1}$. Wave energies were measured with pressure sensors at three 1995 egg loss transects. Triangles represent transect #6, stars represent transect #9 and circles represent transect #2.

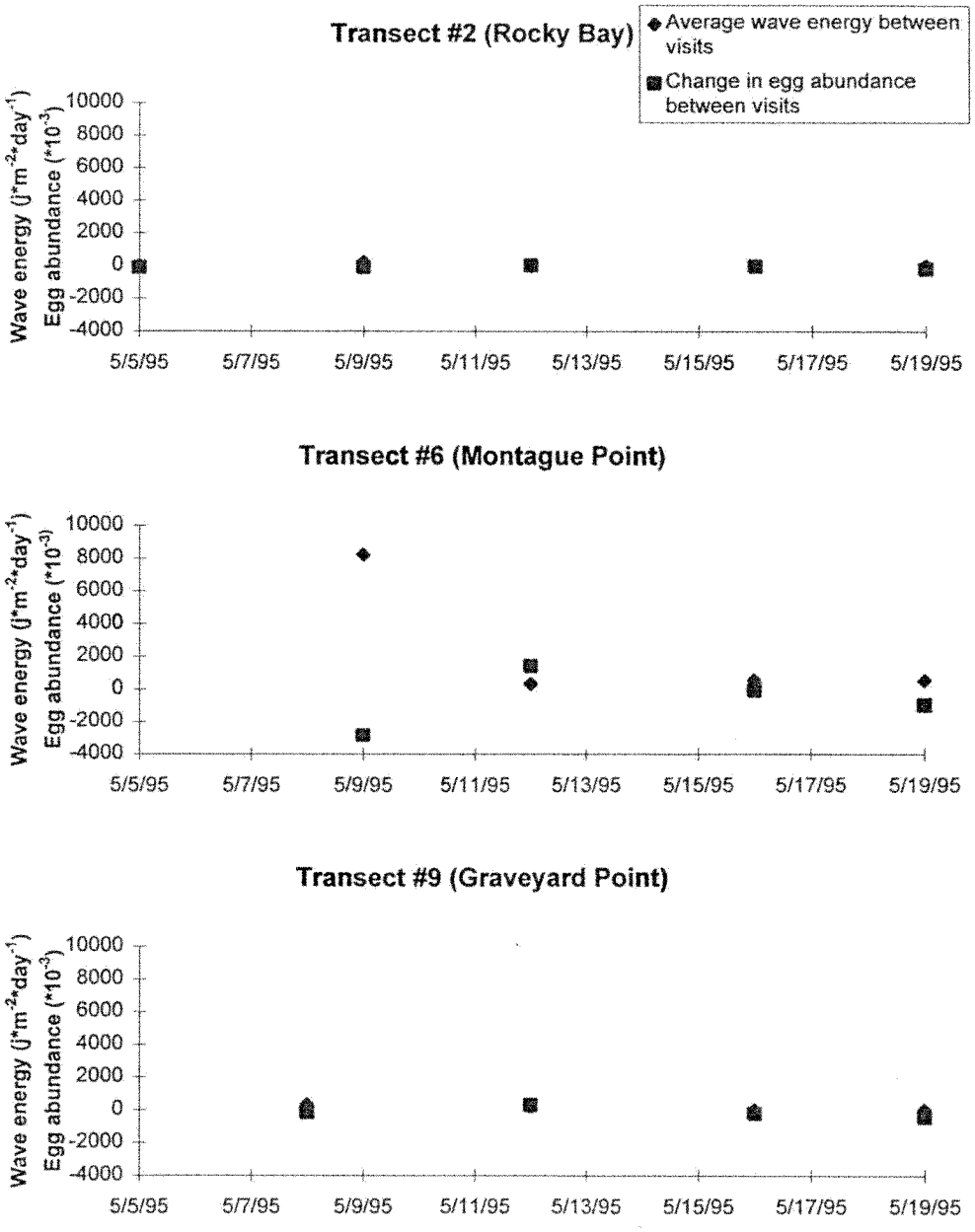


Figure 54. Average wave energy per day and average change in egg abundance between sampling visits against date sampled for 1995 transects.

The analysis of covariance performed on the wave energy data resulted in a good model explaining 34.8% of the variability in the data (Table 41). The covariate, wave energy, was highly significant in predicting changes in egg abundance. Another analysis of variance was performed using high or low energy level as factors to predict the same changes in egg abundance between sampling visits. The high energy level included the points associated with the large storm event recorded at Montague Point, while the low energy level encompassed the remaining points. Energy level was again highly significant in the resulting analysis of variance, explaining 35.1% of the variability in egg abundance (Table 42). Changes at high and low energy levels were significantly different with higher egg loss at the high energy level. The mean loss at the high energy level was 283,873 eggs (SE=33,300), at low energy levels the mean egg loss was 4,083 (SE=4,797).

To test the validity of the wave exposure habitat variable used in egg loss modeling, average wave energy*day^{-1} from the wave energy recorders was compared between the two categories; wave-exposed and wave-protected. The average wave energy*day^{-1} for the exposed transects was 1333.5 joules*m^{-2} (SE=689.4). The average wave energy*day^{-1} for the wave-protected transect was 71.1 joules*m^{-2} (SE=35.6). A t-test of average wave energy*day^{-1} shows that there is no significant difference between the two categories, wave-exposed and wave-protected ($p=0.19$). This may be a function of the wide range of wave energy*day^{-1} measured at each transect resulting in large standard errors calculated for each

Table 41. Results of analysis of covariance to determine the effect of wave energy on egg abundance. Changes in egg abundance between sampling visits was regressed against average wave energy per day between sampling visits.

Analysis of Covariance

Dependent Variable: Change in Ln(egg abundance) between sampling visits

N: 369 Multiple R: 0.590 Squared Multiple R: 0.348

Source	Sum of Squares	DF	MSE	F-Ratio	P
Regression	$181.094*10^{10}$	1	$181.094*10^{10}$	195.828	0.000
Error	$339.387*10^{10}$	367	$0.924760*10^{10}$		

Table 42. Results of analysis of covariance to determine the effect of high or low wave energy levels on egg abundance.

Analysis of Covariance

Dependent Variable: Change in Ln(egg abundance) between sampling visits

N: 369 Multiple R: 0.592 Squared Multiple R: 0.351

Source	Sum of Squares	DF	Mean Square	F-Ratio	P
High energy/low energy	$182.447*10^{10}$	1	$182.447*10^{10}$	198.080	0.000
Error	$338.034*10^{10}$	367	$0.92104*10^{10}$		

category. Wave energy values at the protected transect ranged from 1 to 491 $j*m^{-2}$, and at the exposed transects the range was from 2 to 19,001 $j*m^{-2}$.

Therefore, a nonparametric test of the wave exposure variable using ranks of wave energy$*day^{-1}$ was evaluated. This reduced the variance estimate in each category, while maintaining the relative values of each wave energy measurement. A Mann-Whitney test performed on the ranks of wave energies showed there is a highly significant difference ($p<0.000$) between wave energy$*day^{-1}$ rankings in the two wave exposure categories. Thus, the wave exposure variable used in the model seems to have been justified as being a valid division of transects into two levels of wave action.

3.4. Discussion.

The differences in egg loss between the lower and higher wave energy levels are striking and may imply the existence of a threshold energy level beyond which significant egg loss occurs. The lower energy levels did not have any clear effect on egg loss, which is explainable if the wave energies were not larger than the threshold. The large wave energy recorded at Montague Point associated with egg loss would therefore be above the wave energy threshold. The problem with the data is a lack of observations from intermediate wave energy levels. There is a large gap between the lower energy level ($<600\ j*m^{-2}*day^{-1}$) and the higher energy level ($8229\ j*m^{-2}day^{-1}$). Although the two levels are significantly

different from one another, the existence of a threshold energy level for egg loss cannot be confirmed because of the limited range of wave energy values recorded during the 1995 herring egg incubation period.

Storm events did have a large effect on wave energy levels measured at transect #6, and in turn these resulted in large egg losses, averaging 283,873 eggs per quadrat. Using the egg loss model, an estimated 393,771 eggs per quadrat were initially spawned at transect #6; therefore, 72.1% of the eggs at the transect were removed by the large storm. Hart and Tester (1934) and Hay and Miller (1982) estimated the removal of eggs at 26% and 40% by storms and resulting wave action. Thus, the periodic occurrence of storm events may drastically influence the number of eggs lost during incubation.

Since wave energy was observed to be highly variable, egg loss due to storm events is also highly variable between years, as well as short distances. The results of the factorial analyses indicate that wave energy did not explain variability in egg loss rates (Chapter 1). This is probably because of the variability in storm events from year to year, as well as from site to site. The variable we used in the factorial analyses was unable to reflect these levels of variation in wave energy.

Chapter 4. Consumption of herring spawn by greenling species (*Hexigrammidae*) in Prince William Sound.

4.1. Introduction

Predation is an important process regulating egg survival in marine systems (Bailey and Houde 1989). Pacific herring spawn demersal adherent eggs on shallow subtidal and intertidal substrates; consequently, their eggs are available to a variety of predators throughout incubation. Documented predators of herring spawn include birds, invertebrates, marine mammals and fish (Palsson 1984).

Avian predation is thought to be especially important in Prince William Sound because of the large populations of both migratory and resident birds (Isleib and Kessel 1973, Norton et al. 1990). Other studies have shown that birds can consume a large percentage of the total herring spawn deposited. Avian predators were responsible for over 95% of the Pacific herring egg loss in the intertidal zone in Holmes Harbor Washington in 1946 (Cleaver and Franett 1946). Egg loss due to avian predation accounted for 39% of the total egg loss occurring in the intertidal zone on the west coast of Vancouver Island from 1947-1950 (Outram 1959). Of Pacific herring egg loss occurring in Yaquina Bay, Oregon, 70% was attributed to avian predation in 1970 (Steinfeld 1971). Estimates of bird predation

at two sites in British Columbia were 3.0% and 3.5% of the total spawn deposited by herring (Haegele and Schweigert 1989, Haegele and Schweigert 1991).

Much less is known about the effects of other predators, as studies to quantify Pacific herring egg loss due to nonavian predators are rare. Spawning herring in Barkeley Sound, British Columbia were studied in 1988, where total predation by invertebrates accounted for 13.0% of the total eggs deposited, and marine mammals (mostly humpback whales) consumed 3.0% of the total eggs deposited (Haegele and Schweigert 1989). In 1989 herring egg loss due to epibenthic invertebrates was 4.1% of the total spawn in Georgia Strait, British Columbia (Haegele and Schweigert 1991). These studies outline the important role predation may have as a causative factor in egg loss.

Fish predation on herring spawn has not been studied in the northeast Pacific, and it has not been well documented in the fisheries literature in general (McGurk 1991). No documentation of fish predators of Pacific herring eggs were found, but some studies have been conducted on the deeper spawning Atlantic herring (*Clupea harengus L.*). Historically in the North Sea, abundance of haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*) with stomachs full of Atlantic herring spawn were used as indicators of the concentrations of spawning herring (Hempel and Hempel 1971). Perch (*Perca fluviatilis*) was found to be the most important fish predator consuming herring (*Clupea harengus membras L.*) spawn in the Archipelago Sea (Rajasilta et al. 1993). For spring spawning Atlantic herring off the coast of Norway, egg loss due to haddock consumption

was estimated at 4.2% of the total spawn (Toreson 1991). Total Atlantic herring egg loss due to winter flounders (*Psuedopleuronectes americanus*) at a site in the Northwest Atlantic was not less than 7% of the total spawn abundance (Tibbo et al. 1963).

In 1995, documentation of fish predation and the consequences for herring eggs were examined with the objective of including fish predators in the Prince William Sound egg loss model. The working hypothesis for this part of the egg loss study was that higher mean abundance of fish predators would lead to higher egg loss. A second objective was to estimate potential consumption of herring eggs by fish predators in Prince William Sound.

4.2. Materials and Methods

Field Methods

Sampling with gillnets has previously been used to determine fish predators of Atlantic herring eggs (Rajasilta et al. 1993). To document the fish predators of herring spawn in Prince William Sound, fish were gillnetted and stomach contents examined. Variable mesh gillnets were used to collect fish along predetermined egg loss transects. Strung gillnets 100 feet long and 8 feet deep were set in the subtidal and intertidal zones. For each net, stretched mesh sizes ranged from 1.0 inch to 4.5 inches. Panels of same

size mesh were equal length and depth (20 feet by 8 feet), with a total of five panels per 100 foot net.

Gillnets were set along egg loss transects selected by Alaska Department of Fish and Wildlife personnel prior to the beginning of sampling. By gillnetting along existing egg loss transects, data from captured fish could be related to the egg loss data collected by ADF&G.

Since there were at least four confounded factors which could affect catch at each transect (tide stage, day/night, time of day, time since spawning), a standardized fishing plan was developed for use at each transect. This fishing plan was carried out at one to three transects per day, concurrent with ADF&G sampling of that transect. The standardized fishing plan consisted of two nets set parallel to the shoreline at each transect. The gillnets were bottom set at a distance of 50 to 200 feet from the existing egg loss transect to avoid interaction with the diver activity occurring at the transects. The depths fished depended on the tide stage, at high tide depths fished were; 0 feet and -10 feet, while at low tides depths were; -5 feet at low tide and -10 feet. Logistical constraints limited fishing to one series of gillnet samples centered around the daylight high tide, and one series of samples centered around the daylight low tide. Each series consisted of three one hour sets of the two nets, for a total of six gillnet sets over each tide stage.

Fish caught during sampling were enumerated and identified by species. Information collected for each fish included fork length, time of catch, net soak time, and tide stage of sample. Fish stomachs were removed and preserved in 10% buffered formalin for examination of contents.

Laboratory Methods

Stomach contents were categorized by type of prey (herring eggs, vegetation, crustaceans, etc.), and weighed to the nearest 0.01 gram. Wet weights of each group of stomach contents were recorded, and herring spawn was subsampled to determine the number of eggs per gram. By multiplying the wet weight of the herring spawn contained in each stomach by the number of eggs per gram, the total number of herring eggs in each stomach was determined.

Data Analysis

Catch per unit effort was weighted by the average number of eggs per stomach for each species to form an index of fish predation in the model of 1995 herring egg loss, reported in Chapter 1.

Also, density estimates and daily rations of intertidal fish species were used to estimate the total egg removal by fish predators. Density estimates were available from the *Exxon Valdez* oil spill restoration project for a number of fish species in PWS (Jewett

et al. 1995). The densities were obtained from SCUBA transects of the subtidal zone and were stratified into shallow (2-11 meters) and deep (11-20 meters) regions. The shallow survey data includes the range of depths of egg deposition in 1995.

Estimates of the daily ration of herring egg predators were calculated using the Elliot-Persson model,

$$C_t = \frac{(S_t - S_0 e^{-Rt})Rt,}{1-e^{-Rt}}$$

where C_t is food consumption during daylight hours, R is a known (in this case calculated) gut clearance rate, t is the number of daylight hours and S_t and S_0 are average stomach contents at time 0 and time t respectively (Elliot and Persson 1978). Estimates of stomach contents were obtained from examination of fish caught during gillnet sampling and assumed to be constant over daylight hours. The evacuation rate was calculated from a general relationship of marine and freshwater fish species evacuation rates versus temperature, where

$$R=0.0175T-0.0442$$

(Worobec 1984). The average temperature recorded by a thermister installed at transect 6 on Montague Island was used in this equation. Initial consumption of food at the onset of daylight was calculated according to the Elliot-Persson model using the equation,

$$C_{initial}=S_{average}-(S_0 e^{-Rt}),$$

where $S_{average}$ is the average eggs per stomach from gillnet samples, and t is the nighttime hours. Adding $C_{initial}$ and C_t gives an estimate of the total consumption, C_d, of herring eggs over 24 hours.

Total potential consumption was then calculated by two methods. First total consumption was estimated by

$$C_{total}=C_d*D*I$$

where C_d is the calculated daily consumption in numbers of eggs, D is the predator density, and I is the length of the incubation period in days. Total potential consumption per m^2 was then compared to the average number of eggs per m^2 counted at spawn deposition transects to obtain a percentage of total eggs lost to fish predation.

Another method used to estimate total consumption of herring spawn by greenling was to calculate the amount of eggs eaten as a percentage of greenling body weight. The weight of eggs consumed per day was calculated by converting the daily ration in numbers of eggs to weight of eggs in grams. Then; assuming isometric growth for greenling, and using the end points of greenling length and weight ranges reported in Rosenthal (1980), the weight of each greenling caught during sampling was calculated. Using these two calculations for each fish sampled, the daily ration as a percentage of body weight was estimated.

Then, incorporating biomass estimates for greenling in Prince William Sound from Rosenthal (1980), and the number of incubation days for herring eggs in 1995 the total weight of consumed eggs per hectare was calculated by

$$C_t = B_g * C_w * I$$

C_t is the total biomass of eggs consumed per hectare, B_g is the biomass of greenling, C_w is the daily ration as a percentage of fish weight, and I is the length of the incubation period in days.

4.3. Results

Six fish species were caught during gillnet sampling at egg loss transects: rock greenling (*Hexagrammos superciliosus*), kelp greenling (*Hexagrammos decagrammus*), Dolly Varden char (*Salvilinus malma*), starry flounder (*Platichthyes stellatus*), red irish lord (*Hemilepidotus hemilepidotus*) and great sculpin (*Myoxocephalus polyacanthocephalus*). The most common fish caught were the two greenling species, followed by Dolly Varden and great sculpin (Table 43). Only one red irish lord and starry flounder were caught. Catch per hour fished for all species was relatively low, ranging from 0.009 fish per hour (SE=0.008) for starry flounder and red irish lord to 0.120 fish per hour (SE=0.052) for the greenling species (Table 43).

Table 43. Catch statistics for gillnet sampling at egg loss transects on Montague Island in 1995.

Number of fish caught by gillnetting

Transect	Hours Fished	Greenling (two species)	Dolly Varden	Starry Flounder	Red Irish Lord	Great Sculpin
1	13.80		6	1		
2	14.43		1			
6	13.46	6				
9	13.87	1				1
11	13.53	4			1	1
12	12.25	1				
13	14.56	1	1			
14	14.65					1
	Total	**13**	**8**	**1**	**1**	**3**

CPUE=catch/hour

Transect	Greenling (two species)	Dolly Varden	Starry Flounder	Red Irish Lord	Great Sculpin
1	0.000	0.435	0.072	0.000	0.000
2	0.000	0.069	0.000	0.000	0.000
6	0.446	0.000	0.000	0.000	0.000
9	0.072	0.000	0.000	0.000	0.072
11	0.296	0.000	0.000	0.074	0.074
12	0.082	0.000	0.000	0.000	0.000
13	0.069	0.069	0.000	0.000	0.000
14	0.000	0.000	0.000	0.000	0.068
Average Catch/hour	**0.120**	**0.072**	**0.009**	**0.009**	**0.027**
SE	0.052	0.047	0.008	0.008	0.012

Examination of stomach contents for all species revealed that only greenling and Dolly Varden were consuming herring eggs. All of the greenling stomachs contained herring eggs, while only four of the eight Dolly Varden caught contained eggs (Table 44). The stomachs of other fish species contained a combination of unidentifiable fish and invertebrates. However, it should be noted that in all cases where fish were found in a stomach, eggs were observed to be in the prey fish stomachs. The average number of eggs per stomach for Dolly Varden was 87 (SE=40.4), while for greenling the average was 8,785 (SE=2107.6). The number of herring eggs per greenling stomach increased exponentially with greenling length (Figure 55).

Based on the stomach contents of each fish species caught, only Dolly Varden and greenling were considered in the calculation of the fish predation index for the egg loss model (Chapter 1). The index was computed by multiplying the catch per hour of each species at each individual transect by the average eggs per stomach for that species. By adding the weighted catch per hour of the two species at each transect, an index of the fish predation for each transect was obtained (Figure 56). The weighted catch per hour ranged from zero at transect 14 (where no fish were caught) to 3,916 at transect 6 (where six greenling were caught).

A pattern in greenling and Dolly Varden catch distributions was apparent, as Dolly Varden were caught exclusively in embayments, while all the greenling except one were caught on the outer coast of Montague Island. An estimate of total consumption of

Table 44. Average number of eggs contained in each stomach of gillnetted greenling and Dolly Varden.

Greenling (two species)

Forklength (mm)	Total number of eggs in stomach
194	1842
195	885
228	3361
283	3382
293	7819
295	4327
299	13577
312	2040
314	8488
377	22043
381	10697
394	24572
425	11177
Average eggs per stomach	**8785**
SE	2107.6

Dolly Varden

Forklength (mm)	Total number of eggs in stomach
265	0
265	220
296	0
378	50
388	0
390	286
438	0
444	141
Average eggs per stomach	**87**
SE	40.4

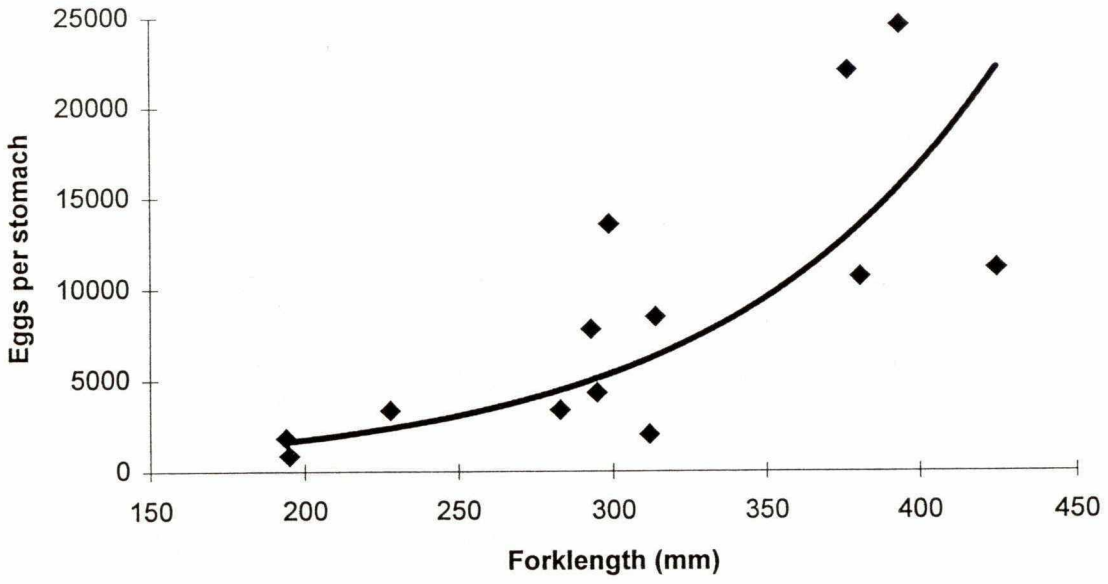


Figure 55. Number of herring eggs per greenling stomach against forklength.

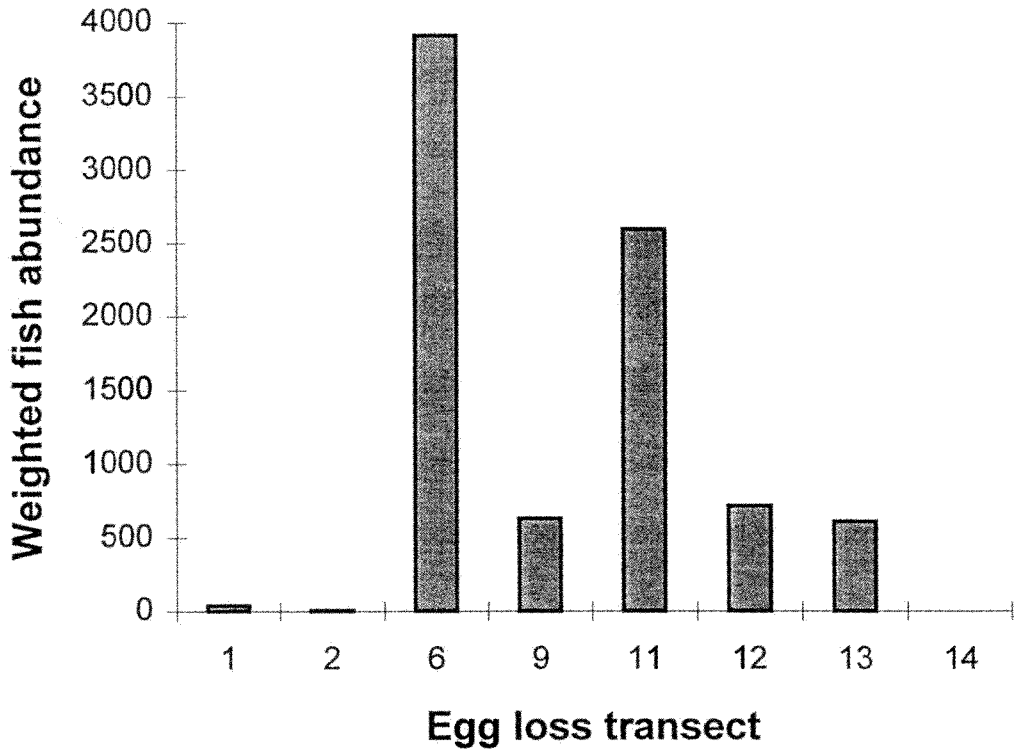


Figure 56. Weighted abundance (catch per hour*consumption) for fish predators at each egg loss transect.

eggs for greenling on the outer coast was calculated using greenling density estimates and daily rations from other studies. The average temperature from a thermister located at -5 ft (relative to mean low water) at transect 6 was 5.8 ^{0}C; resulting in an instantaneous evacuation rate estimate of 0.057 per hour (Worobec 1984). The regression from Worobec (1984) did not include temperatures below 6 ^{0}C, so I had to assume that the relationship would be accurate at the lower temperatures in Prince William Sound. The daily ration calculated with that evacuation rate is 11,984 eggs per day (Table 45).

Subtidal surveys of fish abundance in Prince William Sound found an average of 6.85 greenling per 100 m^2 on island points in shallow waters (depth from 2 to 11 meters) (Jewett et al. 1995). Using the daily ration calculated above, the daily consumption of herring eggs by greenling would be 821 eggs per m^2. In 1995, the incubation period for herring eggs Prince William Sound transects was 21 days, therefore the total removal over incubation would be 17,239 eggs per m^2. The average number of eggs per m^2 calculated using the egg loss model (Chapter 2) on Montague Island headlands was 772,645. Therefore, using the daily consumption estimate from above, 2.23% of the eggs deposited are estimated to be consumed by greenling over the course of incubation.

The weight of the estimated daily ration for greenling (11,984 eggs) was 38.3 grams, or weight of the eggs in a greenling stomach multiplied by 1.29. From this conversion factor, the daily ration as a percentage of greenling body weight was estimated as approximately 6% per day. From dive survey results from Rosenthal (1980), the

Table 45. Calculations for estimating daily consumption of herring eggs by greenling using the Elliot-Persson method.

Elliot-Persson Model for estimating daily consumption

$$C_t=(S_t-S_0e^{-Rt})Rt/1-e^{-Rt}$$

1) Consumption during daylight hours (assuming constant stomach fullness), C	
t=average daylight hours from April 29-May 20, 1995	16.67
Instantaneous evacuation rate (R)=	0.057
S_0	9264
S_t	9264
C_t=	**8816**
2) Initial consumption at onset of feeding=$C_{initial}$	
Decrease in stomach contents during night, $S_t=S_0e^{-Rt}$	
S_0	9264
t=average nighttime hours from April 29-May 20, 1995	7.33
Instantaneous evacuation rate (R)=	0.057
S_t=	6096
$C_{initial}=S_0-S_t$	**3168**
3) Total consumption over 24 hours=$C_{initial}+C_t$	**11,984**

greenling biomass at Zaikoff Point on Montague Island was estimated at approximately 350 kg/ha. Multiplying this biomass estimate by the daily ration as a percentage of body weight and by the number of incubation days (21) in 1995 yields an estimate of egg consumption of 441 kg/ha.

In 1994 an estimate of the biomass of eggs in a 6.4 km stretch of shoreline on Montague Island in 1994 was 5200 kg/km. If you assume that all greenling in a 100 meter band along the shore move in to feed on the eggs deposited in the subtidal and intertidal area, then greenling would consume approximately 8.5% of the total spawn that was deposited there (441 kg of greenling/km of shoreline divided by 5200 kg of eggs/km of shoreline).

4.4. Discussion

The calculation of daily ration by the Elliot Persson method presented here assumes that the greenling are maintaining a full stomach throughout the entire daylight period. Results show that the number of herring eggs per greenling stomach increased exponentially with greenling length (Figure 55). This suggests that our assumption that greenling were maintaining a constant state of gut fullness is correct, since greenling stomach volume should increase exponentially with body length.

Consumption of Atlantic herring eggs by other fish species has been typically estimated at less than 10% of the total herring spawn (Tibbo et al. 1963, Toreson 1991), the same range as estimates found by this study. Although avian predation in the intertidal zone has been estimated at very high levels, 39% (Outram 1958) and 70% (Steinfeld 1971), estimates of consumption by birds as a proportion of the total spawn have been less than 5% (Haegele and Schweigert 1989, Haegele and Schweigert 1991). Benthic invertebrates in Barkeley Sound, British Columbia were observed to consume 13% of the total herring spawn (Haegele and Schweigert 1991). All of these are slightly higher than the estimate found by this study for greenling consumption. However, more species were examined in most of these studies.

Calculation of total consumption of 2.23% of herring eggs spawned in 1995 assumed that there is no numerical response to spawning by greenling from different areas. If the greenling move from deeper water to the band of herring spawn (typically within 5 meters of mean low water), a much higher estimate of consumption is calculated. Jewett et al. (1993) found an average greenling density of 2.04 fish per 100 m^2 in the 11-20 meter depth zone in Prince William Sound. If the entire population in both the deep and shallow zones move into the area of spawn deposition, total consumption of herring eggs would be 5.21%.

The second method for calculating total consumption of herring spawn by greenling resulted assumed that a numerical response was occurring, and resulted in a

higher estimate of consumption, 8.5%. This is probably more realistic since it is likely that greenling would move in to the nearshore zone to feed on eggs.

The estimate of total consumption of herring spawn by fish predators in Prince William Sound from 2.2% to 8.5% is likely to have been underestimated by both methods because the estimate is only for one species of fish. Since greenling make up only 56% by number and 59% by biomass of the fish species at Montague Island (Rosenthal 1980), many other species inhabiting the zone covered by herring spawn, would have access to the rich food source the eggs provide.

Summary

Egg loss in Prince William Sound

The results of this study indicate differences in egg loss arise from differences in depths of spawn distribution with higher egg loss rates at shallower depths (Chapter 1). This trend in egg loss may be the result of increased times of air exposure over the incubation period at shallower depths. Most of the eggs that remain in the spawning beds until hatching are deposited in a range of depths from 0 ft to -10 ft (Chapter 2).

Results also indicate that interannual variability in the strength of environmental factors other than depth may be important. Egg loss caused by wave action is highly variable over time as well as location (Chapter 3). Therefore, in order to obtain high levels of accuracy in calculating herring biomass from egg surveys some measure of egg loss needs to be calculated every year.

Results of the US Forest Service study of egg consumption by bird species indicate avian predators may be responsible for removals of large amounts of spawn (19.4%). Fish predators may remove from 4-8% of total spawn as well (Chapter 4). Thus, predation and highly variable wave action may be the primary causes of egg loss in Prince William Sound.

The different levels of predation in the intertidal and subtidal zones due to birds and fish may be the underlying cause of the higher egg loss rates observed at shallower depths. Egg mortality studies in Prince William Sound indicate mortality may be high at both the

shallowest and the deepest depths where spawn is observed (Debevic 1995). Thus; herring may be spawning at intermediate depths where they can avoid egg losses due to predation, while still maintaining high survival rates until hatch.

Management Implications

In order to accurately estimate the herring biomass in Prince William Sound from spawn deposition surveys, egg loss studies need to be carried out annually. Interannual variability in the effects of environmental factors on egg loss, especially the strength of storms and the abundance of predators needs to be accounted for in each year when estimating the egg loss correction factor. Egg loss studies also need to fully represent the locations and environmental regimes found in the entire area covered by spawn.

If predation is an important factor regulating egg survival to hatching, then herring behavior may lend itself to depensatory mortality. Concentration of herring stocks into a relatively small area during spawning and the resulting spatial concentration of eggs in the spawning beds could lead to high egg losses due to predation even in years of low herring biomass. This in turn could drive the abundance of herring spawn even lower, as predators continued to concentrate on an ever dwindling resource.

The number of eggs spawned each year represents the full potential of recruits to the adult population in future years. Since environmental factors have been shown to influence herring recruitment (Wespestad 1991, Schweigert 1995, Zebdi and Collie 1995)

the egg stage may be an important source of variation in recruitment in some years, if the number of eggs surviving to hatch is influenced by the environmental conditions experienced during incubation.

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